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VARIATION IN *EQUISETUM VARIEGATUM* (EQUISETACEAE: PTERIDOPHYTA)

GAVIN STARK
Woodlands Cottage, Summerbridge, Harrogate,
North Yorkshire, HG3 4BT, England

ABSTRACT

Past authors have recognized a number of forms of *Equisetum variegatum.* This article highlights the large amount of variation within populations of this horsetail resulting from local environmental factors. It is suggested that stem cross-sections are a useful means of distinguishing ecotypes of this species.

INTRODUCTION, METHODS, RESULTS

The statement, "Horsetails are known to be plants of notoriously plastic morphology" Page (1971), will probably prompt a nod of agreement from any botanists who have been involved in their taxonomy. It is reiterated by Hauke (1963) who further notes that this is especially the case for *Equisetum* of sub-genus *Hippochaete. Equisetum variegatum* Schleich. ex Weber & Mohr is one of the two (three including *Equisetum ramosissimum)* British examples of this sub-genus, and certainly a case in point. Various forms of the species have been recorded by authors such as Newman, Milde, Hultén and most recently Page (1982), who in his 'Ferns of Britain and Ireland' distinguishes three British and Irish ecotypes.

The term ecotype was originally coined by Turesson to describe locally distinct races of plants growing in the appropriate habitat. He considered that an ecotype would be produced many times over in circumstances where the same stimuli were acting and thus would not be reliant on colonization of new areas by dispersal only. The principle argument against ecotypes was put forward by authors like Langlet, who suggested that gradual changes in a species should be observed with continuously varying environmental factors. In the case of widespread species this is true; but as Briggs & Walters (1984) point out, "in populations inhabitating two or more very different types of habitat, the pattern of variation in the wild is more likely to be that of distinct ecotypes". In the 'Atlas of Ferns' (1978), Jermy describes the distribution of *Equisetum variegatum* as "A northern-montane species of wet alpine ledges yet also characteristic of sand-dune populations in the west". Thus one might well expect to find an ecotype along the lines of var. *arenarium* (often recorded in older county Floras and on herbarium sheets) as it is a form restricted to the coast. A widespread coastal form is unlikely to have spread through dispersal, but could be an ecotype which has arisen several times over through matching stimuli.

In a small project on variation in *Equisetum variegatum* I visited sites representing four potential ecotypes; these were, sand dunes, inland Irish, upland Northern English and mountain populations in Austria. Data were recorded on the habitat which *Equisetum variegatum* was growing in and the form of the plants.

The great flexibility of form which a single rhizome can produce, so emphasized in Hauke's monograph, was encountered many times over in the field. Take for example a small colony of *Equisetum variegatum*, growing on a well established gravel-bank, about 9m from the edge of the River Tees. The whole bank (an area of some 25m^2) was occupied by a dense colony of *Equisetum variegatum*; but whereas around the edge of the bank stems were upright, on top of the bank, in open stony hollows, stems were decumbent. This marked change in growth form was not an isolated observation: *Equisetum variegatum* stems growing in the base of a dry-stone wall at Malham differed strikingly from those growing nearby, but in the open. The stems in the wall were long, upright, thin and yellow, compared with the short, decumbent shoots found amongst a sparse turf. On the dune

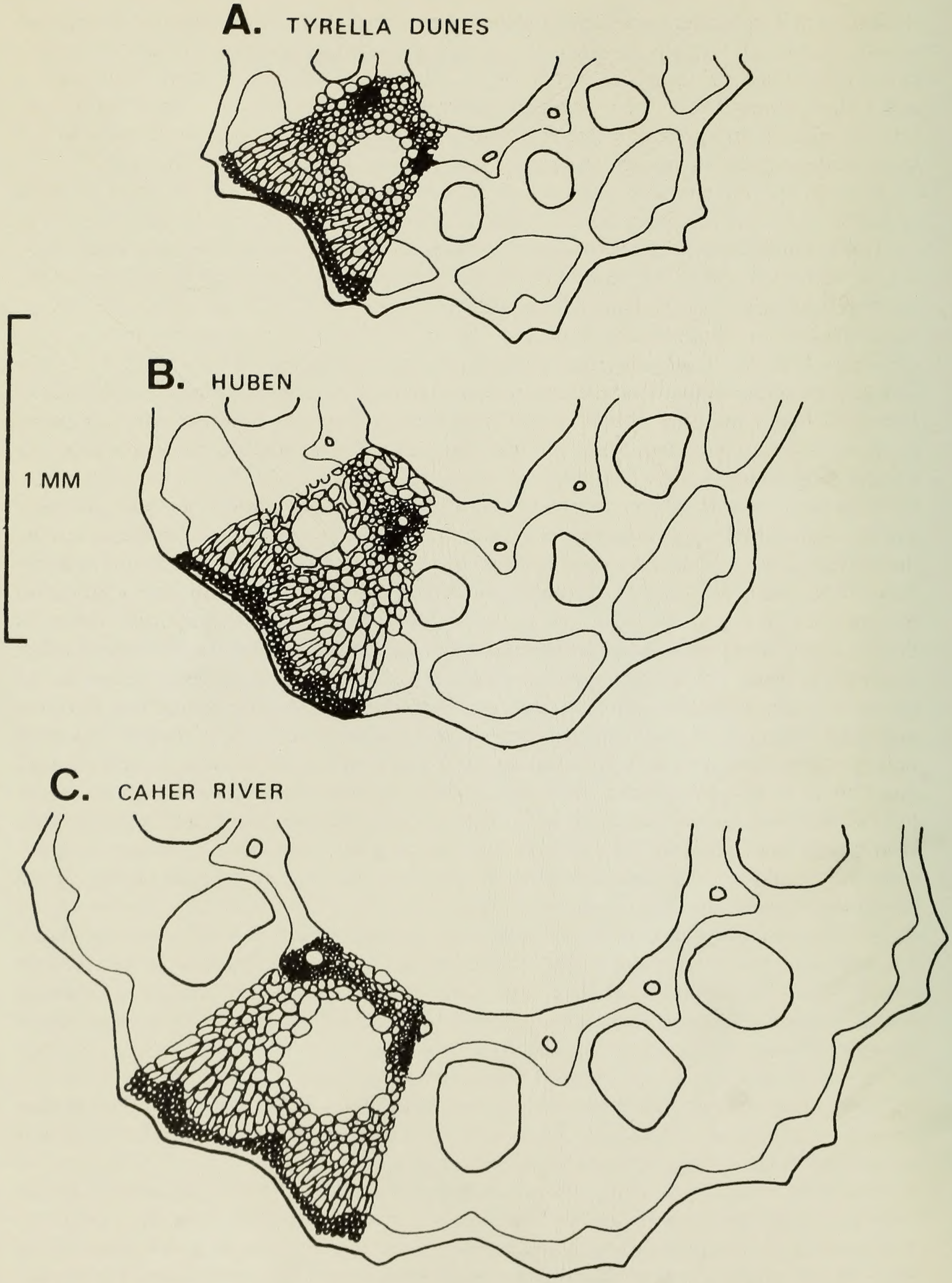

Figure 1. Transverse stem sections of *Equisetum variegatum* from three sites: A) Tyrella Dunes, B) Huben, C) Caher River.

slack floor at Tyrella there were dense patches of prostrate, short, thin *Equisetum variegatum* shoots from which virtually all other species were excluded, gradating into grass dominated sward with occasional upright horsetail shoots. Along the banks of the rivers Rotmoosache and Caher erosion had caused chunks of clayey soil to break off and very often upright tufts of *Equisetum variegatum* grew vigorously from these. This was in contrast to the short, flattened plants growing amongst the closely cropped turf on top of the bank.

It would be ridiculous to call such localized variation ecotype development as these are differences on the microscale. In most cases local environmental factors: trampling, grazing, shading, density of other vegetation, moisture, substrate, base richness and others, can be identified and in one combination or other provide a reasonable explanation for the observed variations. Perhaps the most important effect encountered at the sites visited was the initiation of secondary branching. When a main stem is damaged, two or three secondary branches grow out from the base of the original stem. This was especially the case in dune-slack populations where there was often prolific secondary branching. However, taking on board the great morphological plasticity of *Equisetum variegatum* in response to these factors, the question remains whether definite ecotypes can be distinguished at a wider geographical scale.

Varieties of *Equisetum variegatum* have been described by various authors. An early work is that of Milde (1867) and he recognized some thirteen varieties in Europe, including the coastal form var. *arenarium* and Newman's var. *wilsonii.* The early British pteridologist Edward Newman recognized nine unbranched forms of *Equisetum* which in addition to his var. *wilsonii* included upright and prostrate forms of *Equisetum variegatum.* For both these authors morphological characters were the basis of their definitions: growth habit, dimensions, texture of stems. In the case of both growth habit and stem dimensions the discussion so far has concentrated on the great flexibility of *Equisetum variegatum* rhizomes and the significance of stimuli such as trampling on plants. Var. *wilsonii* is a plant known only from sparse records and a few sites in southwest Ireland but is said to be very distinct, and I think it is significant that the smoothness of the stem is its principle distinguishing feature. In a discussion of two forms of *Equisetum variegatum* at Braunton Burrows, Crabbe et al. (1965) drew parallels between var. *wilsonii* and an upright, robust, smooth stemmed form they found and suggested that microscopic features of the stem epidermis were good diagnostic characters of these plants.

Stem sections were collected and pickled at six of the sites visited but unfortunately when it came to viewing them under the scanning electron microscope the results were disappointing. The epidermis had a very unnatural appearance and neither the stomata nor surface patterning of silica rich materials could be picked out. The epidermis had become damaged at some point; Page (1971) comments that fresh material proved infinitely superior for this work, so it may be the material was stored for too long.

Transverse sections of the stems however showed no sign of damage to the surface or of having dried out. Two or three stems were sampled from each site and the results proved to be interesting. Sections from the two Austrian sites although very different in the field were surprisingly similar in their cross-sections and distinguishable from the British and Irish sites. Stems from the Caher River site were also distinct but those from the Northern England and Northern Ireland sites were not. Put in simple geographical terms the evidence from the six sites sampled suggests distinct European, British and Irish forms. Figure 1 shows some drawings of these stem sections; the number of ridges, their prominence and degree to which they are biangulate (ie. indented) are features to note.

SUMMARY

On the basis of the sites visited (see Table 1) I would conclude that the morphological grounds for separating ecotypes of *Equisetum variegatum* were slim. On the other hand it would seem as though cross sections and possibly microscopic characters could be used, at least to aid taxonomists where local environmental influences are strong.

TABLE 1

Details of sites visited. First the site name and location is given, then the source from which the site was discovered.

Aberffraw, V.C. 52, Anglesea, North Wales. 'Atlas of Ferns'. Visited on the 18th June 1990.
Caher River, V.C. H9, County Clare, Ireland. Herbarium sheets, British Museum (Natural History), 1935 and 1936. 'Sandy bank of Cahir River, near the Bridge, Near Formoyle'. Visited 22nd August 1989.
Huben. Near Langenfeld, Otztal, Austria. Luck. Visited 3rd July 1989.
Malham, Great Close Mire. V.C. 64, North Yorkshire, England (905663). Suggested by Bouckley JH, Chairman, Leeds and District Fern Group. Visited 9th September 1989.
Muckross Lake. V.C. H2, 6km south of Killarney town, County Kerry, Ireland. Herbarium sheet, Edinburgh Botanic Garden, 1981. Specimen of *Equisetum variegatum* var. *majus* from south side of lake; though, after long search, this not refound. *Equisetum* × *trachyodon* on north lake shore and on peninsula. Visited 27th August 1989.
Rosses Point. V.C. H28, County Sligo, Ireland. Herbarium sheet, Edinburgh Botanic Garden. Visited 9th August 1989.
Ross Links. V.C. 68, Northumberland, England (1338). Suggested by Page C.N., Edinburgh Botanic Garden. Visited 2nd December 1989.
Rotmoostal Valley. Near Obergurgl, Otztal, Austria. Found by Huntley B., Botany Dept., Durham, during fieldwork. Visited 11th July 1989.
Teesdale, V.C. 66, County Durham, England (903279). Graham G.G., 1988. 'Confined to the region around Widdybank and down the Tees as far as Middleton. Winch Bridge, 1892, Nowers J.E.' Visited 20th September 1989.
Tyrella Dunes. V.C. H38, County Down, Northern Ireland. Suggested by Hackney P., after his paper, 1981. Visited 31st August 1989.

ACKNOWLEDGEMENTS

Special thanks for his encouragement to A.C. Jermy, for locality suggestions from J.H. Bouckley, G.G. Graham, P.Hackney, B. Huntley, C.N. Page and also to the trustees of the Greenfield Fund, who were kind enough to make available financial assistance for the project.

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MILDE, E. 1867, Monographia Equisetorum. *Nov. Act. Acad. Leop-Carol 32(2).*
PAGE, C.N. 1988, *A Natural History of Britains' Ferns.* Collins, London.
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FERN RUSTS IN MID-WALES AND THE CONJUROR OF CHALGRAVE

RAYMOND G. WOODS
Tymaur Mill, Llanfihangel Brynpabuan, Builth Wells, Powys, Wales

Adrian Hick and Thomas Preece provided some fine scanning electron microscope photographs in the *Fern Gazette* 13 (6) 1990 of fern rusts, yet information on their distribution is sparse. Searching for them in mid Wales in recent years suggests some species are widespread, even turning up on ferns grown in the garden.

Fortunately the damage they cause seems to be minimal and at worst produces somewhat premature brown patches on fronds in the autumn.

Most rust species appear to be commonest in damp and shady sites. It may, however, be that spores are produced more abundantly under these conditions and since it is the tiny white ribbons of spores on the back of fronds, looking like toothpaste squeezed out of a tube, which provides the most obvious evidence of the rust, they are easier to see in damp sites. Covering a Common Polypody offset with a polythene bag to encourage rooting can produce spectacular results if it happens to be infected with *Milesina dieteliana.* The whole of the back of the frond can appear as if sprinkled with icing sugar after a few weeks in the bag. Planted out in the garden new young growth seems unaffected and small brown patches which develop as the fronds reach old age may alone betray the presence of a rust to the casual observer. This species is widespread, if not common, in Brecknock and Radnor.

The commonest rust is *M. kriegeriana* on Common Buckler Fern. Search old, but just living, fronds in any damp woodland or hedge bank where this fern is abundant in the spring and the rust should be found. It is widespread in Cardiganshire, Carmarthenshire, Brecknock, Radnor and Montgomeryshire. It also infects the Male Fern, but is far less common. On the Scaley Male Fern it is very rare and I have only seen it in Devon. This varying abundance may well be related to the degree of winter evergreenness of the fronds. Could deciduousness have developed as a way of thwarting rust fungi?

Soft Shield Fern in mid Wales occasionally sports the rust *M. whitei.* This also attacks, but very rarely, Hard Shield Fern. Until this last summer I had come to think that this rust might be useful to help separate those forms intermediate between Hard and Soft Shield Fern as most infected plants, even if superficially looking like Hard Shield, on close inspection turned out to have some Soft Shield Fern characters. A large population of both species together with intermediate forms in Erwood Dingle, near Builth Wells closely examined this summer showed all to be infected.

Most spectacular of all the fern rusts is *Hyalopsora polypodii.* It is frequent in mid Wales, where it turns the back of Brittle Bladder Fern fronds a bright orange-brown. Also common and conspicuous is *M. scolopendrii* on Hart's Tongue Fern. It produces large circular brown patches with, on the underside of the frond, the tell-tale white ribbons of spores. Less obvious, but equally widespread is *M. blechni* on Hard Fern. It, like nearly all fern rusts, seems to prefer damp places. Still to find are the rarer species on Wall Rue, Beech and Oak Fern.

The budding pteridologist might also, to spare a blush, keep an eye open for the result of the Rust *Tranzschelia anemones*; this has long been known as The Conjuror of Chalgrave's Fern; there is a picture (Fig. 1) in Ray's Synopsis, ed. 3, 1724, and the story goes farther back to Hoffmann (1662) and Thalius (1585); J. Ramsbottom (Trans.Brit.Myc.Soc. 4, 1913) gives a detailed summary of the story. It attacks Wood Anemone, and in the process elongates the leaves into a very fern-like state and completes the delusion with a crop of dark brown, sorus-like clusters of spores on the underside of the leaves (Fig. 1).

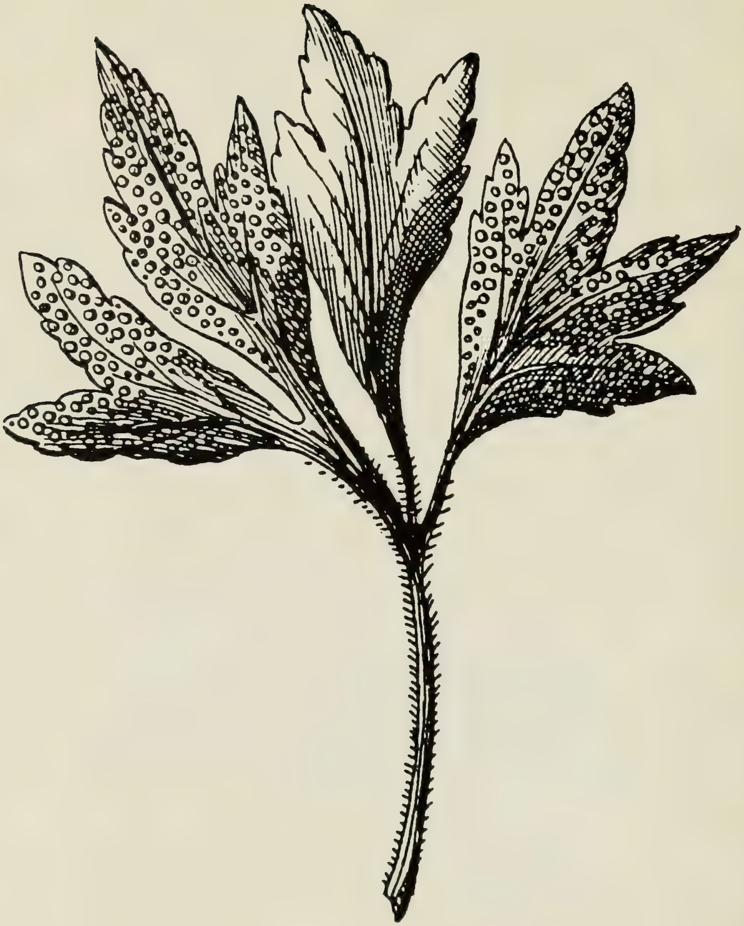

Figure 1. The Conjuror of Chalgrave's Fern *Tranzschelia anemones* on *Anemone nemorosa,* from Ray, Synopsis Methodica Stirpium Britannicarum, ed. 3, 1724, Tab. III, fig. 1.

DRYOPTERIS × *FURADENSIS* (DRYOPTERIDACEAE: PTERIDOPHYTA) A NEW ENDEMIC FERN HYBRID FROM MADEIRA

H. WILFRIED BENNERT
Spezielle Botanik, Ruhr-Universität Bochum, Universitätsstrasse 150,
D-4630 Bochum 1, Germany

HELGA RASBACH & KURT RASBACH
Dätscherstraße 23, D-7804 Glottertal, Germany
&
RONALD L.L. VIANE
Leerstoel voor Morfologie, Systematiek en Ecologie van de Planten,
Rijksuniversiteit Gent, K.L. Ledeganckstraat 35,
B-9000 Gent, Belgium

ABSTRACT

A new *Dryopteris* hybrid from Madeira is described as *D.* × *furadensis.* We report on its cytology and on several micromorphological characters that were investigated in order to establish its putative parents. Most probably the endemic species *Dryopteris aitoniana* Pichi Serm. and *D. maderensis* (Milde) Alston were involved in the origin of the new hybrid.

INTRODUCTION

As in other groups of pteridophytes, hybridization is not uncommon in the genus *Dryopteris* (see the listing of Knobloch 1976). Hybrids are known to occur not only between more common and widespread *Dryopteris* species but also between rare or even locally endemic taxa. For the fern flora of the Macaronesian Islands which is especially rich in endemic *Dryopteris* species (see Hansen & Sunding 1985) it has been shown that hybridization not only gives rise to single sterile hybrid individuals but may also act as an efficient promotor of speciation (Gibby 1983, 1985; Gibby et al. 1977, 1978). This has been demonstrated for the origin of the allotetraploid species *Dryopteris guanchica* Gibby et Jermy and *D. crispifolia* Rasbach, Reichstein et Vida. Whereas in the Canary Islands and especially in the Azores a number of *Dryopteris* hybrids were discovered and described (Fraser-Jenkins 1981, 1982; Gibby & Widén 1983; Gibby & Fraser-Jenkins 1985) none were previously known from the Island of Madeira (see Manton et al. 1986). In the following we describe a new endemic diploid *Dryopteris* hybrid from this island for which we propose the name *Dryopteris* × *furadensis*; it was discovered during an excursion to Madeira in the summer of 1988 (see below).

In Madeira four *Dryopteris* species occur, two of which are endemic and two more widespread: *Dryopteris aemula* (Aiton) Kuntze has a distinct Atlantic distribution, extending to all major groups of the Macaronesian Islands except the Cape Verde Islands (Jalas & Suominen 1972, Hansen & Sunding 1985). The apomictic species *D. affinis* (Lowe) Fraser-Jenkins is widely distributed in Europe; in Madeira only the diploid subsp. *affinis* is present. *D. aitoniana* Pichi Serm. is endemic to Madeira; it is a relatively isolated species of which no close relatives are known. According to its gross morphology, it is closer to *D. filix-mas* and the *D. villarii* group than to the other *Dryopteris* species occurring in Madeira; its phytochemistry (phloroglucinol composition) is in spite of some similarities quite distinct from that found in *D. filix-mas* (von Euw et al. 1985). If it is accepted as a distinct species, *D. maderensis* (Milde) Alston is also endemic. *D. maderensis, D. azorica* (Christ) Alston from the Açores, and *D. intermedia* (Mühl.) A. Gray from North America differ slightly in their morphology, but their genomes are homologous; therefore these three taxa are to be regarded as very closely related (Gibby & Walker 1977). Because of the corresponding morphology, Fraser-Jenkins reduced *D. maderensis* to a subspecies of *D. intermedia* but keeping *D. azorica* as a separate species (Fraser-Jenkins 1981, 1982). We follow the older taxonomy and treat *D. maderensis* as a species.

MATERIALS AND METHODS

Spores were examined using a small portable microscope. This method (Bennert et al. 1990) allows identification of hybrid plants in the field by their aborted spores. The single hybrid plant discovered (see below) was collected living and has been cultivated since then in the greenhouse of the Botanical Garden at Bochum for further investigations.

For **cytological analyses** premature sporangia were fixed using a mixture of acetic acid and ethanol (1:3). Preparations were made following the classical method of Manton (1950: 293).

The method for obtaining epidermis preparations suitable for studying **leaf micromorphology** and the terminology applied for describing glands and multicellular hairs were expounded by Viane (1986, 1990).

Generally, **cell dimensions** in (allo-)polyploid taxa are not exactly medial between the corresponding values of their ancestral taxa as Barrington et al. (1986) and Viane (1986) have independently shown. A "polyploidy factor P" has to be used in these cases (Viane 1988; Rasbach et al. 1989; Viane 1990), a procedure that may often help in checking putative ancestry. However, on a theoretical basis and departing from the general formula that has to be applied in allopolyploid taxa (for details see Viane 1990), cell dimensions in diploid hybrids are, with some restrictions, medial between those of their diploid ancestors. If we assume the P factor to be the same (or nearly so) in the two diploid species with the genome formulas AA and BB, then the cell dimensions (indicated as $|AB|$) of the hybrid AB (no polyploidisation has occurred!) can be simply calculated according to the following equation:

$$|AB| = \frac{|AA| + |BB|}{2}$$

As *Dryopteris* × *furadensis* is a diploid hybrid (see below), this formula can be applied if we assume the P factors of the parents involved to be equal. As three different Madeiran diploids (*Dryopteris aemula* [Ae], *D. aitoniana* [Ai], and *D. maderensis* [Ma], see below) are to be taken into consideration as parent species, three hybrid combinations are theoretically possible: AeAi, AeMa, and AiMa. The dimensions of several micromorphological characters (uniserate multicellular hairs, glands and stomata) were analyzed for all three diploid species and for the hybrid *D.* × *furadensis*. On the basis of these measurements and applying the formula given above, the expected mean cell dimensions were calculated for the three possible hybrid combinations quite simply as the means of the values of the possible ancestral species. These predicted values were compared with those actually measured in *D.* × *furadensis*. There was no obvious congruency between the actual hybrid and one hybrid combination with respect to the whole set of data studied. Therefore a number of multivariate cluster analyses (distance: 1-Pearson Correlation Coefficient, unweighted pair-group method using arithmetic averages or UPGMA) were applied and tree diagrams generated. This method is appropriate for estimating phenetic relationship and taxonomic resemblance; details are documented and discussed by Sneath & Sokal (1973).

RESULTS AND DISCUSSION

During an excursion to Madeira made in July and August 1988 by three of us (W.B., H.R. and K.R.) selected areas were carefully studied for ferns. Several new finds were made, among them first records of two taxa (*Asplenium adiantum-nigrum* and *A.* × *ticinense*) for Madeira (see Rasbach et al. 1990).

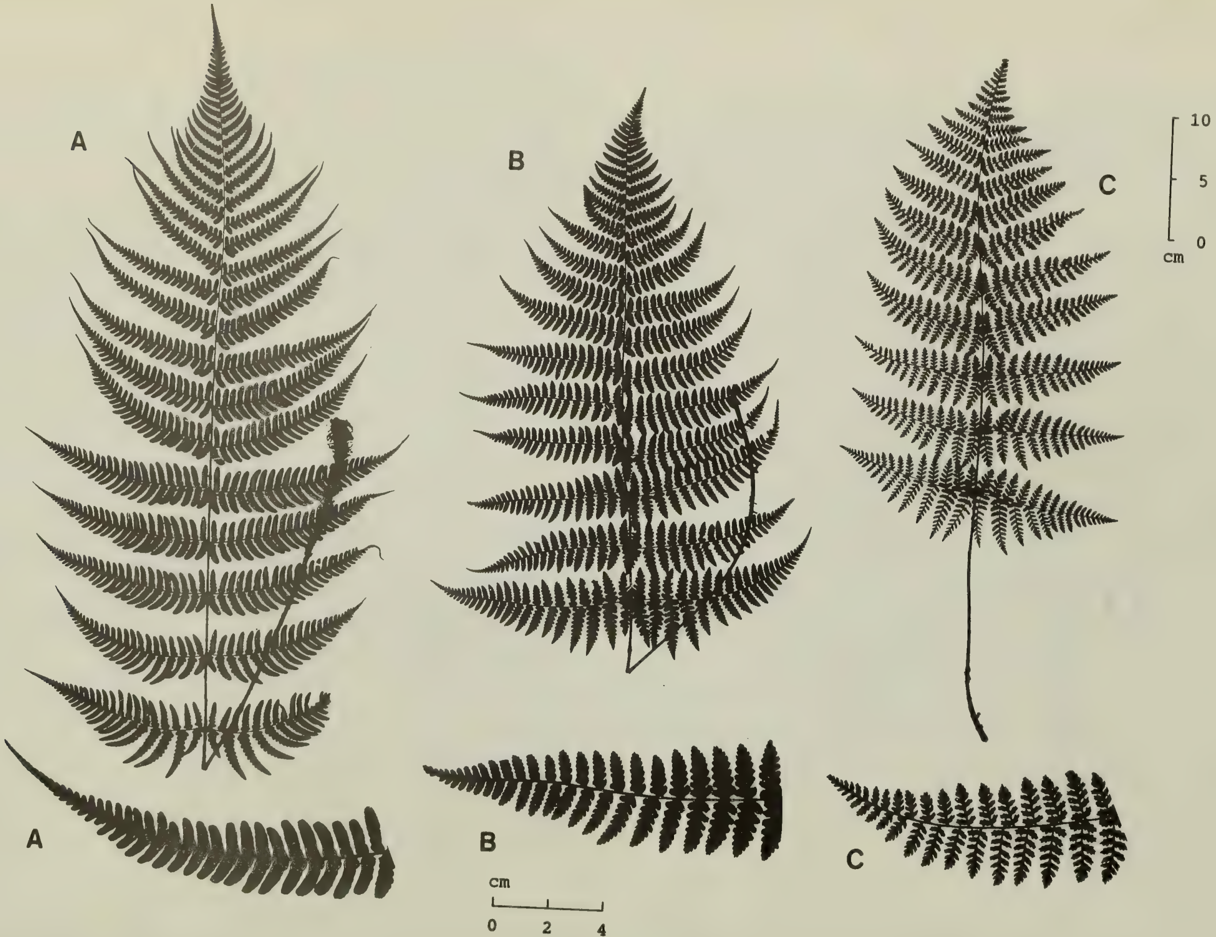

Figure 1. Silhouettes of fronds and pinnae of *Dryopteris* × *furadensis* and its parent species. A: *Dryopteris aitoniana* (WB SP 70/88, above Levada do Furado, Madeira, 30.7.1988), B: *Dryopteris* × *furadensis* (WB 71/88, above Levada do Furado, Madeira, 30.7.1988), C: *Dryopteris maderensis* (WB 166/88, above Levada do Furado, Madeira, 16.8.1988).

On 30 July 1988 the vicinity of Ribeiro Frio was explored, a place that is famous for its wealth of fern species and the luxuriant growth plants show in suitable stations (see Benl 1971). Our special interest was attracted by the laurel forest vegetation of which relatively well-preserved areas are present above the Levada do Furado, especially in small ravines that are kept moist even in summertime by continuously running or at least dripping water. In such a favourable place all four Madeiran *Dryopteris* species (*D. aemula, D. affinis, D. aitoniana,* and *D. maderensis*) were found growing together in abundance. A careful search revealed the presence of a hybrid plant that in its gross morphology was intermediate between *D. aitoniana* and *D. maderensis* (Fig. 1).

Diagnosis

Dryopteris* × *furadensis Bennert, Rasbach, Rasbach & Viane ***hybr. nov.***

Planta hybrida, morphologia inter parentes praesumptos intermedia. Lamina fere triangularis ad ovata, usque 45 cm longa. Stipes squamis brunneis sparse vestitus, usque 35 cm longus. Pinnae illis *Dryopteridis maderensis* similes, sed angustiores et longiores, pinnulae minus profunde incisae et minus acute dentatae. Indusium tholiforme, subcoriaceum, illi *Dryopteridis aitonianae* simile, sed minus firmum et modo sparse glanduligerum. Sporae abortivae. Planta diploidea, meiosi paribus 0 vel 1 et univalentibus 80-82.

Holotypus: Madeira, steep slope of a ravine above the Levada do Furado w of Ribeiro Frio, c. 920 m alt., coll. H.W. Bennert, C. Bennert, H. Rasbach & K. Rasbach, 30 July 1988. BM. Isotypes: B, COI, M and Z.

Hybrid plant intermediate in its morphology between its putative parents. The lamina is subtriangular to ovate and up to 45 cm long. The stipe is sparsely clothed with brown scales and up to 35 cm long. The pinnae are similar to those of *Dryopteris maderensis* but smaller and longer, with less deeply cut and less acutely toothed pinnules. Indusium dome-shaped, somewhat coriaceous, similar to that of *Dryopteris aitoniana*, being, however, less firm and bearing only scattered glands. Spores abortive. Diploid plant with 0 to 1 pairs and 80-82 univalents at meiosis.

The plant is named after the "Levada do Furado" in whose vicinity it was found.

Cytology

As usual in fern hybrids, meiosis is disturbed and leads to completely irregular tetrads with several unevenly sized nuclei (Fig. 2). The meiotic pairing behaviour of chromosomes is shown in Fig. 3. 82 univalents are visible, bivalents are lacking. In another cell studied 1 pair and 80 univalents were found. Thus it becomes clear that the hybrid is diploid and must have originated from a cross between two likewise diploid and unrelated species. This result is comparable to the cytology found in another diploid *Dryopteris* hybrid, namely *Dryopteris* × *vidae* (= *D. pallida* subsp. *pallida* × *D. villarii* subsp. *villarii*) (Fraser-Jenkins & Gibby 1980). It also shows exclusively univalents or only few chromosome pairs (up to 4).

For the Island of Madeira 4 *Dryopteris* species, all diploid, are recorded (see Introduction): *D. aemula, D. affinis, D. aitoniana,* and *D. maderensis* (Hansen & Sunding 1985). As *D. affinis* is an apomictic species, any hybrid derived from it should be triploid. For this reason *D. affinis* can be safely ruled out as a parent of *D.* × *furadensis*. Unfortunately, no further conclusions as to the origin of *D.* × *furadensis* can be drawn from the cytological result. All other hybrid combinations would also yield diploids and would most likely show a very similar pairing behaviour at meiosis. The interpretation of the parentage is therefore based on morphological characters only (see the following paragraph).

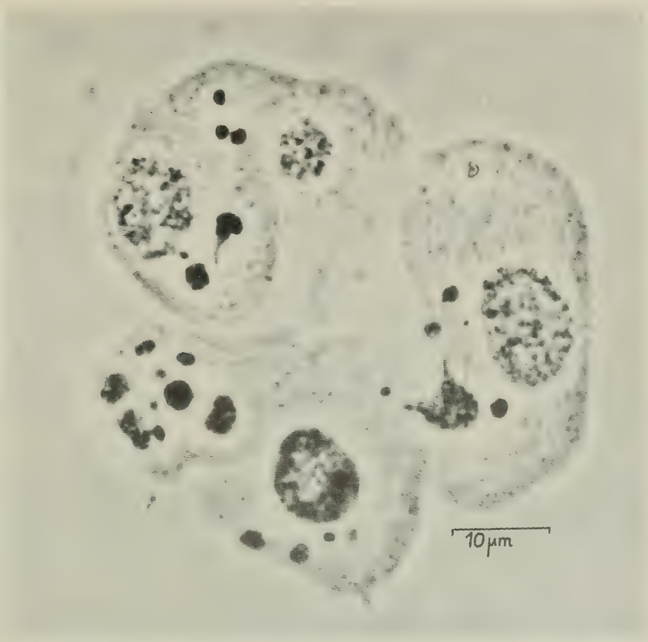

Figure 2. Cytology of *Dryopteris* × *furadensis* (WB SP 43/88). After the second meiotic devision a completely irregular tetrad with several unevenly sized nuclei is formed. Consequently, only aborted spores develop. (Preparation and photograph by H.R.).

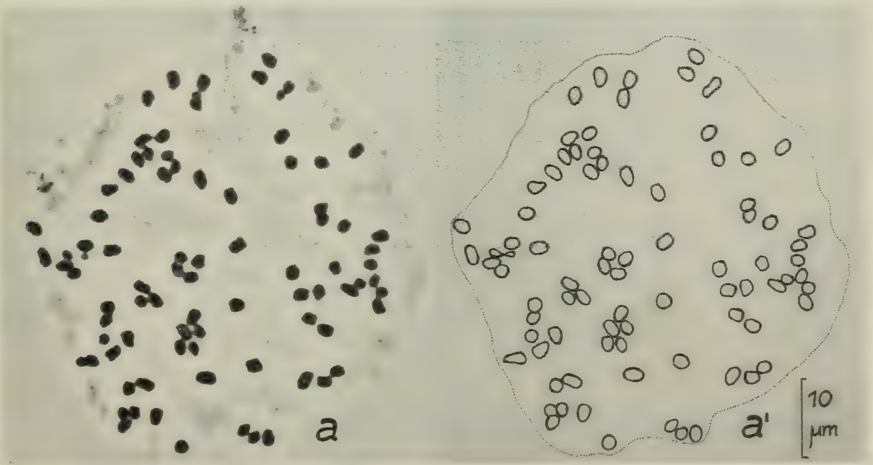

Figure 3. Cytology of *Dryopteris* × *furadensis* (WB SP 43/88). Spore mother cell in meiosis showing n = 82^{I} (only univalents). a: photograph, a': explanatory diagram (det. H.R.).

Micromorphology

In all taxa investigated, uniseriate multicellular hairs are present. There is a considerable variation between species of all characters measured (Table 1). In Table 2 the predicted mean hair dimensions for the three hypothetical hybrid combinations are compared with the data obtained for *D.* × *furadensis*. It is evident that there is no hybrid combination whose complete data set would conform to that of *D.* × *furadensis.* Numerical analysis (tree diagram not shown) reveals, however, that the hairs of *D.* × *furadensis* are twice as similar to those predicted for the hybrid between *D. aitoniana* and *D. maderensis* as to those of the two other hybrid combinations.

TABLE 1

Dimensions of uniseriate multicellular hairs (mean ± standard deviation in µm). Lt = overall hair length, N = number of cells per hair, Lc = length of upper cells, Wc = width of upper cells.

Taxon	**Lt**	**N**	**Lc**	**Wc**	**Lc/Wc**
D. aemula	210-360-510	7-10-13	29-39-49	18-23-28	1.3-1.7-2.1
D. aitoniana	243-321-400	6- 8-10	39-49-59	30-37-45	1.0-1.4-1.7
D. maderensis	369-462-556	9-12-15	34-44-54	39-46-53	0.7-1.0-1.2
D. × *furadensis*	214-351-488	7- 9-11	36-45-54	31-37-43	0.9-1.2-1.5

TABLE 2

Predicted mean dimensions (µm) of uniseriate multicellular hairs for three hypothetical hybrid combinations and measured values for *D.* × *furadensis* (abbreviations see Table 1); Ae = 1 genome of *D. aemula*; Ai = 1 genome of *D. aitoniana*; Ma = 1 genome of *D. maderensis.*

Genome combination/ taxon	**Lt**	**N**	**Lc**	**Wc**	**Lc/Wc**
AeAi	340.5	9	44.0	30.0	1.46
AiMa	391.5	10	46.5	41.5	1.12
AeMa	411.0	11	41.5	34.5	1.20
D. × *furadensis*	351.0	9	45.0	37.0	1.21

Table 3 summarises the data obtained for the length of the laminar glands. Again, there is considerable variation between species, especially for total length. In Table 4 the predicted mean gland dimensions for three hypothetical hybrid combinations are compared with the values of *D.* × *furadensis.* As for the hair data, it is not possible to designate a certain hybrid combination in which the whole set of data would conform with that found in *D.* × *furadensis.* Again, the method of cluster analysis was applied (cluster tree not shown). It shows that the unicellular glands of *D.* × *furadensis* are most similar to those predicted for the hybrid between *D. aitoniana* and *D. maderensis.* Mean gland length (lT), and consequently also mean length of the stalk (lS), are smaller than expected (Table 4); perhaps the expression of the character "laminar glands" by the genome of *D. maderensis* is poor. Apparently, both dA and the shape descriptors dA/lS and dA/dB are in this case better indicators of affinity.

TABLE 3

Dimensions of laminar glands (= unicellular hairs) (mean ± standard deviation in µm); lT = total length, dA = diameter of the apex, dB = diameter of the base, lS = length of the stalk.

Taxon	**lT**	**dA**	**dB**	**lS**	**dA/lS**	**dA/dB**
D. aemula	46-53-57	40-43-46	13-15-17	8-13-17	2.5	2.9
D. aitoniana	52-62-72	22-25-27	11-14-16	28-37-46	0.7	1.8
D. maderensis	109-124-139	24-31-38	17-22-27	79-93-107	0.3	1.4
D. × *furadensis*	70-78-86	23-27-30	14-15-17	44-51-59	0.5	1.8

TABLE 4

Predicted mean dimensions (µm) of laminar glands for three hypothetical hybrid combinations and measured values for *D.* × *furadensis* (abbreviations see Table 3); Ae = 1 genome of *D. aemula; Ai* = 1 genome of *D. aitoniana*; Ma = 1 genome of *D. maderensis.*

Genome combination/ taxon	**lT**	**dA**	**dB**	**lS**	**dA/lS**	**dA/dB**
AeAi	57.5	34	14.5	25.0	1.36	2.3
AiMa	93.0	28	18.0	65.0	0.43	1.6
AeMa	88.5	37	18.5	53.0	0.69	2.0
D. × *furadensis*	78	27	15.0	51.0	0.52	1.8

TABLE 5

Stomata length (µm), as well as sporangial and indusial indument.

Taxon	**Stomata**	**Glands on sporangium stalk**	**Indument of indusium edge**
D. aemula	39-44-49	uni- or multicellular	glands and hairs
D. aitoniana	38-41-44	mostly unicellular	glands
D. maderensis	36-40-43	absent	glands
D. × *furadensis*	30-34-38	absent	glands

TABLE 6

Predicted mean of stomata length (µm), and expected sporangial and indusial indument for three hypothetical hybrid combinations and data for *D.* × *furadensis*; Ae = 1 genome of *D. aemula*; Ai = 1 genome of *D. aitoniana*; Ma = 1 genome of *D. maderensis.*

Genome combination/ taxon	**Stomata**	**Glands on sporangium stalk**	**Indument of indusium edge**
AeAi	42.5	uni- or multicellular	glands and hairs
AiMa	40.5	some unicellular or none	glands
AeMa	42.0	some uni- and multicellular or none	glands and hairs
D. × *furadensis*	34.0	none	glands

In all taxa the stomata are uniformly polocytic. Other characters studied are length of the guard cells as well as indument of the sporangium stalk and of the indusium margin (Table 5). Table 6 shows the predicted stomata size and the expected indument for three hybrid combinations in comparison with the characters of *D.* × *furadensis.* The guard cell size of the new hybrid is much smaller than expected. The absence of uniseriate hairs on the margin of the indusium may indicate that no genome of *D. aemula* is present in the hybrid (otherwise the character must be suppressed).

Finally, all micromorphological data were analysed simultaneously in a single cluster analysis (distance: 1-Pearson Correlation Coefficient, UPGMA) (Fig. 4). Evidently, this analysis confirms the previous results and shows the closer relationship (distance = 0.546) between the indument characters of the new Madeiran hybrid and those predicted for a hybrid between *D. aitoniana* and *D. maderensis.* When all taxa are analysed together with the predicted hybrid, a tree results (Fig. 5) that again confirms the proposed ancestry.

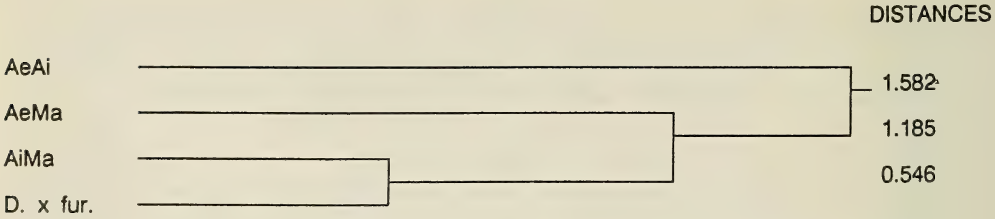

Figure 4. Phenogram (on the basis of all micromorphological characters analysed) showing the similarity between *Dryopteris* × *furadensis* and the three theoretically possible hybrid combinations. Distance metric is 1-Pearson Correlation Coefficient. Ae = 1 genome of *D. aemula*; Ai = 1 genome of *D. aitoniana*; Ma = 1 genome of *D. maderensis* (computed by R.V.).

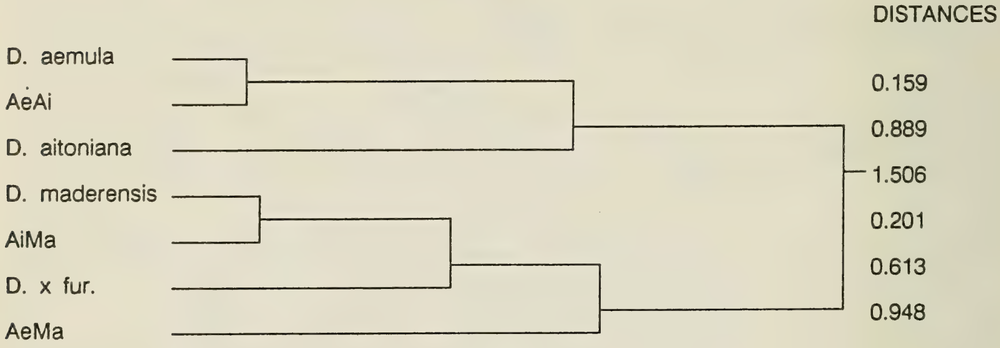

Figure 5. Phenogram (on the basis of all micromorphological characters analysed) showing the similarity between *Dryopteris* × *furadensis*, the three Madeiran diploids, and the three theoretically possible hybrid combinations. Distance metric is 1-Pearson Correlation Coefficient. Ae = 1 genome of *D. aemula*; Ai = 1 genome of *D. aitoniana*; Ma = 1 genome of *D. maderensis* (computed by R.V.).

ACKNOWLEDGEMENTS

We thank Prof. Dr K.U. Kramer (Zürich) for his help in correcting the manuscript and the Latin diagnosis. The help of Mrs I. Künzel, Bochum, with photographic work and of Mrs S. Hoeper, Bochum, with some computer problems is gratefully acknowledged.

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CORRIGENDA

The following photographs and diagrams were inadvertently not up to standard in *Gazette* 13 (7) pages 375, 386, 388 and 393. They are here repeated of better quality.

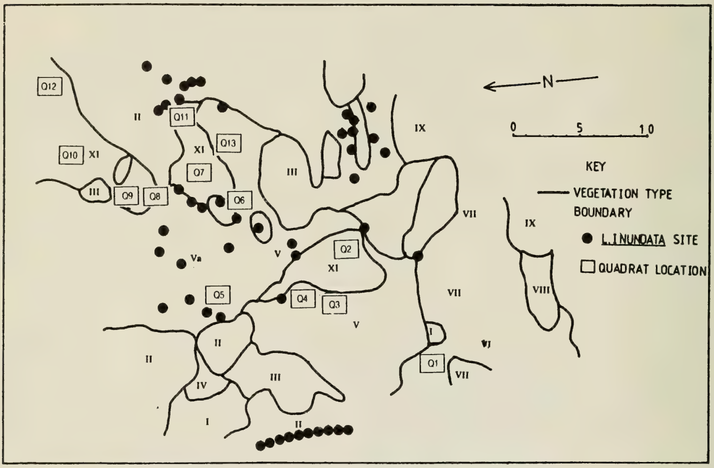
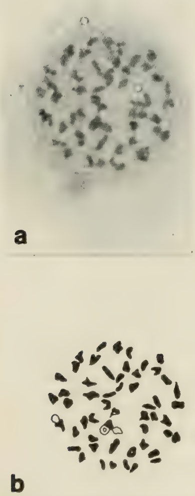
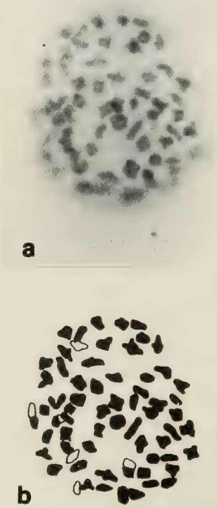


Figure 3. South Pit – vegetation types (scale in metres).





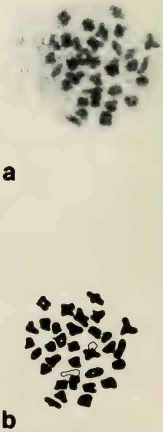


FIGURE 1: a) Metaphase I in *G. bancroftii*, x 1000. b) Explanatory diagram showing 56 bivalents.

FIGURE 2: a) Metaphase I in *G. costaricensis*, x 1000. b) Explanatory diagram showing 68 bivalents.

FIGURE 3: a) Metaphase I in *G. bifida*, x 1000. b) Explanatory diagram showing 34 bivalents.

continued on page 24

ISOETES × HICKEYI (ISOETACEAE: PTERIDOPHYTA) IN CANADA

DANIEL F. BRUNTON
216 Lincoln Heights Road, Ottawa, Ontario K2B 8A8, Canada
&
DONALD M. BRITTON
Department of Molecular Biology and Genetics,
University of Guelph, Guelph, Ontario N1G 2W1, Canada

ABSTRACT

The recently described *Isoetes* × *hickeyi* is considered to be the hybrid between *I. echinospora* and *I. macrospora.* Despite the large sympatric ranges of the putative parents the hybrid has been reported only from the type locality in Wisconsin, U.S.A. This paper reports six new populations from eastern and central Canada and provides additional ecological, morphological and distributional data. These support our expectation that this taxon is likely rare but regularly occurring across a wide range in northern North America.

INTRODUCTION

Recent studies of quillworts (*Isoetes*; Isoetaceae) in North America have disclosed that hybridization is possible between many aquatic North American species under laboratory conditions (Boom 1982; Luebke & Taylor 1985). Cytological and electrophoretic evidence further suggests hybrids also occur in the wild as well where two or more species grow together. Natural interspecific hybrids include *I.* × *eatonii* Dodge [*I. echinospora* Dur. × *engelmannii* A. Br.], *I.* × *hickeyi* Taylor & Luebke [*I. echinospora* × *macrospora* Dur.], *I.* × *dodgei* Eaton [*I. echinospora* × *riparia* Engelm.], *I.* × *brittonii* Brunton & Taylor [*I. engelmannii* × *riparia*], and *I.* × *jeffreyi* Britton & Brunton [*I. macrospora* × *riparia*] (Taylor & Luebke 1985; Taylor & Luebke 1988; Britton & Brunton 1989; Brunton & Taylor 1990; Britton & Brunton 1991, respectively).

Isoetes × *eatonii* is the best known of these hybrids, occurring in many sites across northeastern North America (Kott & Bobbette 1980 pers. obs.). Experimental results suggest that these hybrids produce sterile spores (Boom 1982, Taylor & Luebke 1985). Some hybrids such as *Isoetes* × *eatonii* and *Isoetes* × dodgeii, however, are found in populations numbering into the thousands of plants (Varga 1988 pers. obs.). *Isoetes* × *hickeyi* is the only one of this group known from only a single population. It is reported from a site in northern Wisconsin where it grows with its putative parents, *I. echinospora* and *I. macrospora (I. lacustris L, pro parte)* (Taylor & Luebke 1988). Accordingly, limited ecological, morphological and distributional data have been described for this taxon. Given the wide zone of overlap of the putative parents (across the Canadian Shield of Canada from eastern Manitoba to the Atlantic coast and through much of New England in the United States – cf. Kott and Britton 1983; Cody & Britton 1989) we expected it to be found in a number of other sites in the United States and Canada.

Reports of hybrids are becoming more common in North America (Taylor & Luebke 1985; Taylor & Luebke 1988, Britton & Brunton 1989; Brunton & Taylor 1990; Britton & Brunton 1991) and it seems reasonable to expect that reports from elsewhere in the world will soon appear. In Great Britain, for example, *Isoetes echinopora* and *I. lacustris* grow together and are suspected of producing sterile hybrids (C. Jermy, pers. comm.). If one accepts the view that *I. macrospora* is the North American synonym for *I. lacustris* then the product of such hybridization would be *I.* × hickeyi.

This paper reports the results of our search for additional North American locations for *I.* × *hickeyi* and provides new morphological, site ecology and distributional information for that taxon.

MATERIALS AND METHODS

Recent studies of *Isoetes* herbarium specimens in OAC, ACAD, NYS, TRT, NSPM, PSU, DAO, CAN and Brunton's personal herbarium (DFB) revealed a number of suspected hybrid specimens which were identified by their irregularly formed megaspores (Figure 1). Mixed populations of *I. echinospora* and *I. macrospora* were also surveyed for hybrids in 15 locations in southern Ontario and southern Quebec during the summers of 1988-1990.

Spore samples of a number of the suspected hybrids were air dried and attached to the 16 SEM stubs with double-sided scotch tape, sputter coated with gold palladium and examined with a JEOL 35C Scanning Electron Microscope (SEM).

Sizes were calculated from the SEM photographs and from tracings of SEM projections for a selection of spores. SEM distorts these images to some degree and so the resulting size data are taken as approximations.

Chromosome counts of the hybrid were made from root tip squashes of the Buttermilk Falls, Haliburton County and Island 397, Regional Municipality of Muskoka, Ontario populations [*Brunton 9327A; Brunton 9327B; M.J. Sharp, s.n.*]. Plants were grown at Guelph in distilled water in a growth cabinet. The developing root tips were excised and pretreated in saturated aqueous paradichlorobenzene (PDB) at room temperature for 4 hours. They were then washed in distilled water, fixed in acetic alcohol (three parts absolute ethyl alcohol to one part glacial acetic acid), hydrolysed in Warmke's solution (one part concentrated HCL to one part absolute ethyl alcohol) for 7-10 minutes, and stained in leucobasic fuchsin (Feulgen) for two hours. The meristems were squashed under a coverglass in 45% acetocarmine stain and examined.

RESULTS

Status and habitat

Six new populations of *I.* × *hickeyi*, all from Canada, are identified in this study (Figure 1). They are as follows:

Manitoba

Seal River, west of Great Island, [ca. 58° North, 96° West], 8 July 1956, *J.C. Ritchie s.n.* (TRT 236871) – five plants with two *I. macrospora*; 3 July 1956, *J.C. Ritchie 1868* (TRT 236868) – one plant with two *I. macrospora*.

Nova Scotia

Colchester County, North end of Economy Lake at tiny island at UTM 327368 (National Topographic Series map 11 E/5), 3 September 1990, D.F. Brunton and K.L. McIntosh 10,137B (OAC, DFB) – three plants with *I. macrospora* and *I. prototypus*).

Ontario

Haliburton County, Stanhope Township, north end of Boschkung Lake at Buttermilk Falls, Kennisis River, 10 August 1989, *D.F. Brunton 9200A* (OAC, DFB) – 5 plants; 24 August 1989, *D.F. Brunton 9327A* (OAC, DFB) – three plants with one *I. echinospora*; 24 August 1989, *D.F. Brunton 9327B* (OAC, DFB) – one plant with numerous *I. macrospora*; [Guilford Township], Gull River at the picnic area on the west side of West Guildford [sic], 13 September 1989, *P.M. Catling and J. Norris 10039* (DAO 582174k); 13 September 1990, D.F. Brunton 10,215B (OAC, DFB) – one plant with *I. echinospora* and *I. engelmannii*; Regional Municipality of Muskoka, Georgian Bay Township, in Twelve Mile Bay, southeast shore of Island 397, Georgian Bay Islands National Park UTM NV 736932, 31 July 1990, *M.J. Sharp, D. Hart & V. Sahanatien, s.n.* (OAC) – one plant with *I. echinospora* and *I. macrospora*.

Quebec

Pontiac County, Onslow Township, north shore of Ottawa River 3 km southeast of Beech Grove, 10 September 1987, *B. Di Labio s.n.*, (OAC, DFB) – two plants with four *I. macrospora*.

Twenty-three plants of *I.* × *hickeyi* have been identified in these collections, usually found with plants of *I. macrospora* and/or *I. echinospora.* All but the Quebec plants were found in submerged sites, usually in running, cold, oligotrophic, slightly acidic water in clean sand or gravel substrates with only sparse associated bottom vegetation. Most plants were from disturbed waterways (e.g. those in Haliburton County) or in back eddy areas below faster water (e.g. the Pontiac County, Quebec site and at the Buttermilk Falls, Haliburton County, Ontario locality). The majority of plants were found growing in water between 0.4 and 1.5m deep, although the plant in Pontiac County, Quebec was emergent (Brunton & Di Labio 1989) and those at the Seal River, Manitoba station included individuals growing at 2.0m depth.

Gross morphology

The gross morphology of particular *Isoetes* species is notoriously variable depending on subtle changes in environmental and site conditions (Eaton 1990; Britton & Kott 1983). Accordingly, it is difficult to be categorical about gross morphological characteristics. Comparisons between hybrids and their parent species are possible on a site-by-site basis, however. Hybrid vigour, resulting in larger, more robust individuals, is common in many hybrids (cf. Britton & Brunton 1989). This was evident at most of these newly reported *I.* × *hickeyi* stations. Individuals of the parent species were clearly smaller in stature in the Pontiac County, Quebec, and the Ontario stations (except at the West Guilford, Haliburton County site). Many of the hybrid plants also support significantly more leaves than the plants of the accompanying parent species. A sampling of plants at the hybrid locations provided the following average numbers of leaves: 18.1 for *I.* × *hickeyi* (n = 16), 16.0 for *I. macrospora* (n = 16) and 9.9 for *I. echinospora* (n = 15).

Spore morphology

The plants identified as *I.* × *hickeyi* all demonstrated spore morphology that is intermediate between that of *I. echinospora* and *I. macrospora* (Figures 2, 3, 4). Most match the illustrations of the type specimen in Taylor & Luebke (1988) very closely *viz.*, polymorphic, frequently aborted and sterile megaspores of intermediate size with a dense pattern of high, convoluted ridges and spines on the triradial hemisphere, a narrow band of papillae below the equatorial suture and a dense pattern on convoluted, high-walled ridges ("brain coral") on the distal hemisphere (Figures 2 and 3).

The Buttermilk Falls, Ontario population also contained plants which showed strong tendencies towards the spore morphology of one or the other parent. Some of the Buttermilk Falls plants have megaspore sizes averaging larger than most *I.* × *hickeyi* megaspores and also exhibit an open pattern of shorter ridges and a more distinct equatorial band of papillae that is strongly suggestive of *I. macrospora.* Others at Buttermilk Falls contained smaller than average spores and a disproportionate number of single spines and columns, virtually no equatorial band of papillae and fewer, shorter convoluted, high-walled ridges. These plants indicate their hybrid nature by an abundance of polymorphic, aborted spores of variable size.

Microspores examined from several of the collections (Figure 4) also exhibited intermediate characteristics between the putative parents. Microspores from the Seal River, Manitoba and Beech Grove, Quebec sites averaged 35.3 um (n = 80), intermediate between the mean of 42 um for *I. macrospora* and 26 um for *I. echinospora* (Kott & Britton, 1983) and similar to the microspore size (34 um) determined at the type locality (Taylor & Luebke 1988).

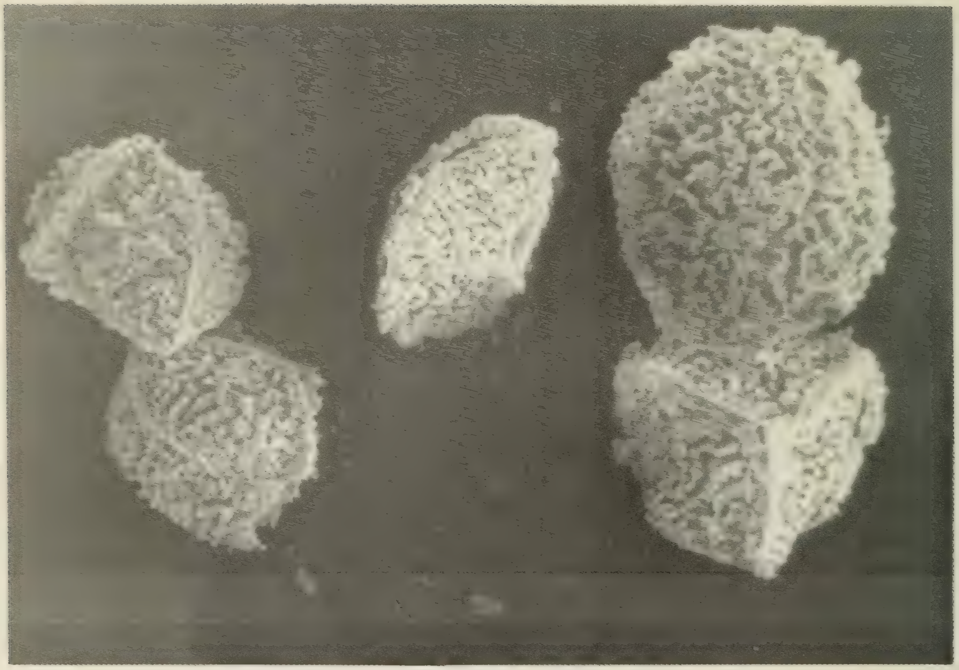


FIGURE 1: Megaspores of *I.* × *hickeyi* (Brunton 9327A (OAC), Bar = µm). Note variable size, distorted shape and irregular surface ornamentation typical of *Isoetes* hybrids.

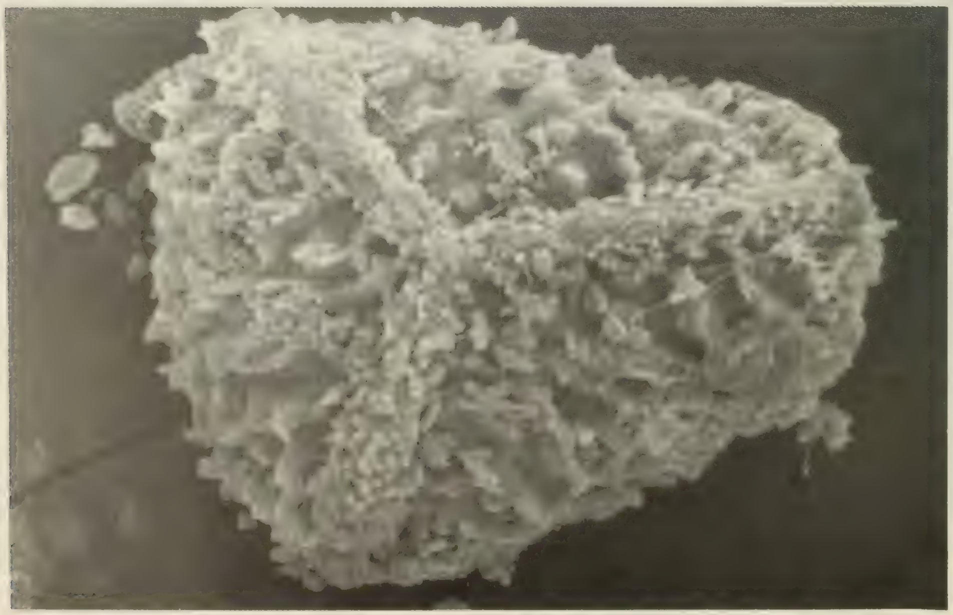


FIGURE 2: SEM photomicrograph of triradial hemisphere of *Isoetes* × *hickeyi* megaspore (Bruntor 9327A (OAC), Bar = 100µm).

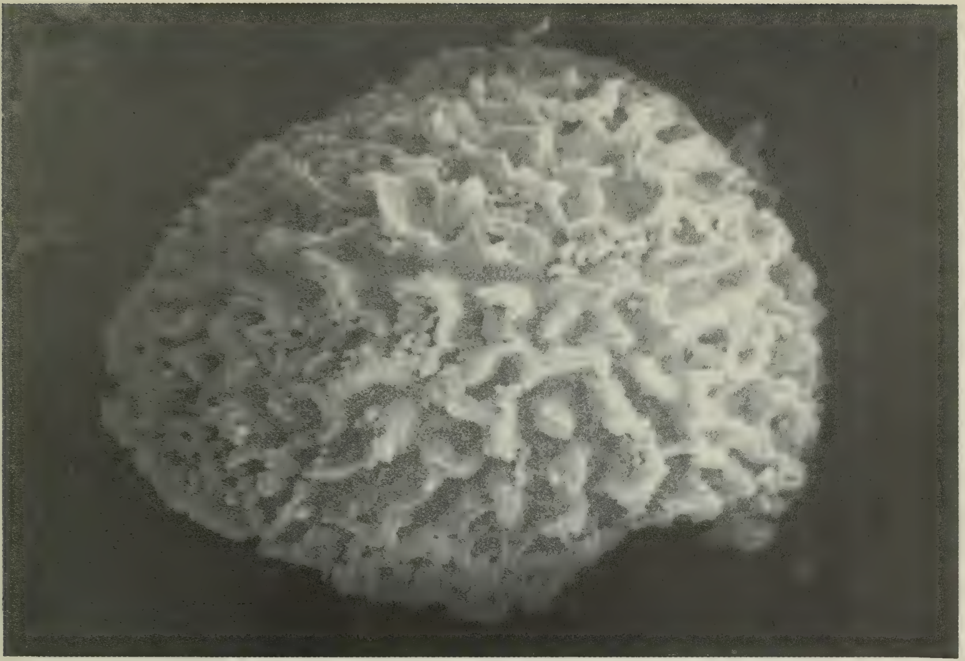


FIGURE 3: SEM photomicrograph of distal hemisphere of *Isoetes* × *hickeyi* megaspore (Brunton 9327A (OAC), Bar = 100 µm). Note narrow band of papillae by the equator.

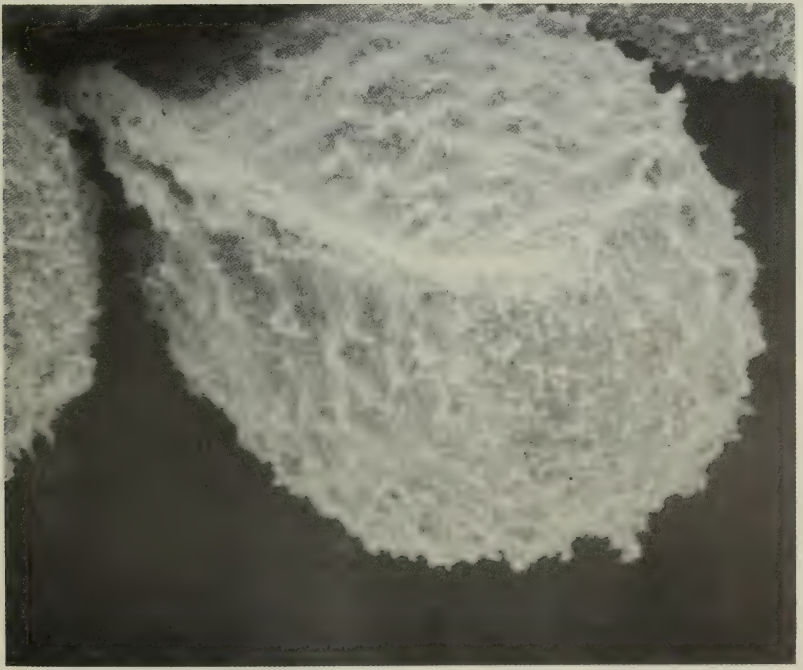


FIGURE 4: SEM photomicrograph of microspore of *Isoetes* × *hickeyi* (Di Labio, s.n. (OAC), Bar = 11 µm).

Cytology

Chromosome counts were undertaken for a number of plants from the Buttermilk Falls and Island 397, Ontario location. Plants with 'typical' *intermediate I.* × *hickeyi* spore morphology, as well as those with *echinospora*-like and *macrospora*-like megaspore morphology were examined and found to be 2n = 66, as is expected for a hybrid between *I. macrospora* (2n = 110) and *I. echinospora* (2n = 22) (Kott & Britton 1983). Vouchers for these are preserved as OAC.

DISCUSSION

Isoetes × *hickeyi* would appear to be a regularly occurring but rare hybrid throughout the sympatric range of its putative parents, *I. echinospora* and *I. macrospora*. Although the degree of spore abortion is not as great as that in other *Isoetes* hybrids such as *I.* × *dodgei* or *I.* × *jeffreyi* (Britton & Brunton 1989, Britton & Brunton 1991) thus suggesting a higher possible level of fertility, it is found mostly in small populations of one to a few plants in large populations of either or both of the putative parents. Most hybrids occur at sites where substrate disturbance by wave action, accelerated current, high rate of sedimentation, etc. is atypically great. This presumably increases the concentration of free-floating spores and enlarges the potential for physical contact between microspores and megaspores of different species.

Taylor & Luebke (1988) recorded no germination in their laboratory trials of *I. echinospora* × *I. macrospora*. At the Buttermilk Falls, Ontario and (possibly) Seal River, Manitoba stations, however, *I.* × *hickeyi* plants are thought to be numerous. This suggests locally efficient reproduction in some manner, perhaps occurring by apomixis. To date, however, apomixis has not been detected in North American *Isoetes* (W.C. Taylor, J. Hickey, pers. comm.).

While a consistent intermediate megaspore morphology appears to be typical of most plants, megaspore morphologies strongly reflecting that of one or the other putative parents are found. This morphological variation may result from differing combinations of parental spores, *viz.*, male *I. macrospora* and female *I. echinospora* and *vice versa*.

ACKNOWLEDGMENTS

Our thanks to the curators of the herbaria consulted for the opportunity of examining material in their care and to B.M. Di Labio, Ottawa, Ontario and M.J. Sharp, Guelph, Ontario for their specimens. We also thank G.W. Argus for the use of working space and optical equipment for Brunton at the Canadian National Museum of Nature, Ottawa. Other valuable assistance and data were provided by K.L. McIntosh, Ottawa, Ontario, D. Metsger, Royal Ontario Museum, Toronto, Ontario and R.J. Pittaway, Minden, Ontario. We also thank the National Science and Engineering Council of Canada for their financial support for the second author.

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REVIEW

PROCEEDINGS OF THE INTERNATIONAL SYMPOSIUM ON SYSTEMATIC PTERIDOLOGY edited by K.H. Shing & K.U. Kramer. 330 pp. 1989. ISBN 7-5046-0151-9/Q.5. China Science and Technology Press, Beijing.

This is the published papers of the Symposium held in Beijing on 5-10 September 1988, nicely presented as a hard-bound volume. It has been edited with care and attention to detail by Kramer and Shing. The original idea for a Symposium in China was born in 1978 when the reviewer was able to visit Professor R.C. Ching, eminent pteridologist and 'grand old man' of Chinese botany. The timing of the meeting was to celebrate Ching's 90th birthday, but alas he passed away in July 1986. As preparations were well advanced the Symposium commemorated his life and work and this volume opens with a review of Ching's contribution by another nonagenarian, R.E. Holttum; and K.H. Shing, long-time student of Ching and his successor in Beijing, reviews pteridological research in China – past and present.

The 50 papers that follow are grouped into General, Biosystematics, Geography, Ecology and floristics. Morphology and anatomy, Chemistry and medicine, and Palaeobotany. It would be invidious to select any individual papers for comment; authors from 11 countries have contributed and it is good to see the work of over 40 Chinese pteridologists getting into print. A volume reprinting 12 of the more substantial papers, with a full bibliography of all of Ching's work was published by the Academia Sinica, Beijing (ISBN 7-03-00753-O/Q 121) in 1988 to link with the Symposium.

A.C. JERMY

CORRIGENDA

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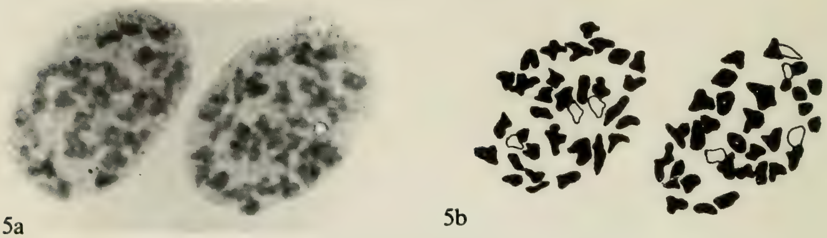

FIGURE 5:
a) Metaphase 1 in two cells of *G. retroflexa*, x 1000.
b) Explanatory diagrams showing 34 bivalents in each cell.

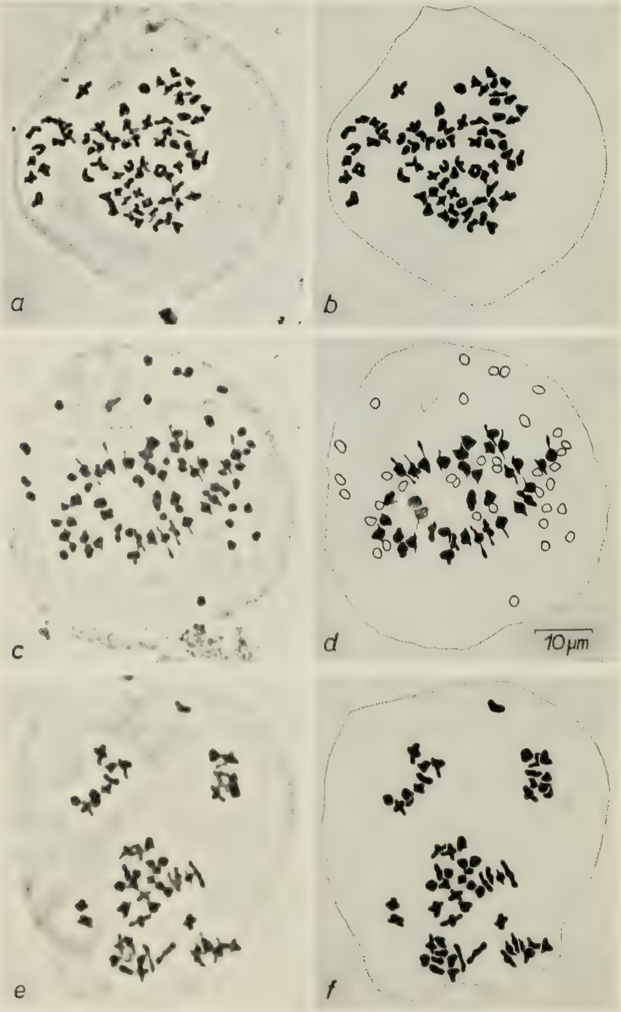

Figure. 2. Cytology (spore mother cells in meiosis) of some Madeiran ferns. a) and b) *Asplenium adiantum-nigrum* (Ras-660), a) photograph, b) explanatory diagram showing 72 bivalents; c) and d) A. × *ticinense* (WB SP-27/88), c) photograph, d) explanatory diagram showing 36 univalents and 36 bivalents, pairs black, univalents outlined; e) and f) *Cheilanthes tinaei* (Ras-652), e) photograph, f) explanatory diagram showing 60 bivalents.

DIVERSITY, ECOLOGY AND DISTRIBUTION OF HIGH-ELEVATION PTERIDOPHYTES WITHIN RIO ABISEO NATIONAL PARK, NORTH-CENTRAL PERU

KENNETH R. YOUNG[1,2] & BLANCA LEON[2]
[1]Department of Geography, University of Colorado,
Boulder, CO 80309, U.S.A.; and [2]Museo de Historia Natural,
Av. Arenales 1256, Apartado 14-0434, Lima 14, Peru

ABSTRACT

The upper elevations (2300-4200m) of a national park located on the eastern slopes of the northern Peruvian Andes were surveyed for their pteridophyte flora. A total of 174 species in 43 genera were found. The most diverse ecological zone was the montaine rain forest zone located from 3100m upwards to timberline, which contained 109 pteridophyte species. This was high species richness compared to adjacent ecological zones: tropical alpine, 65 species; montane wet forest, 61 species. We suggest that reasons for this were a high and constant humidity, the abundance of speciose genera such as *Elaphoglossum*, and the sharing of species with both of the adjacent zones.

INTRODUCTION

Peru has a rich pteridophyte flora estimated at about 1000 species (Tryon & Stolze 1989a). Country-wide flora treatments now appearing (Tryon & Stolze 1989a, 1989b) will soon provide a uniform base for evaluating the regional distribution of pteridophyte taxa and diversity.

As a complement to regional studies, landscape-scale studies carried out over a restricted area of hectares to tens of square kilometers in size are also important as it is possible therein to examine the relationship of pteridophyte diversity to both habitat diversity in the landscape and habitat preferences shown by the pteridophytes. Only two such studies have so far been completed in Peru: one done by León & Valencia (1988) in montane vegetation on the western slopes of the Andes, and another by Young & León (1989) in lowland forests of the Amazon basin. In this article, we report on the pteridophytes of the high-elevation vegetation types of a site located on the eastern side of the Peruvian Andes. We documented species diversity in a number of ecological zones, examined habitat diversity within each zone, and looked for possible explanations for the presence of differing pteridophyte growth forms in each zone.

STUDY AREA AND METHODS

Rio Abiseo National Park is located in the Department of San Martin on the Eastern Cordillera of the Andes of northern Peru (Fig. 1). The Park contains elevations from 700-4200m, and thus protects a diverse range of vegetation types from lowland rain forest to tropical alpine vegetation (Leo and Ortiz 1982; Young & León 1988).

Beginning in 1985, the Park has been the object of intensive plant collecting at altitudes greater than 2300m. Young & León (1990a) recently summarized this information, listing full or tentative identifications, and giving complete documentation of voucher herbarium specimens and elevational ranges for each taxon within the Park.

For the present study, we analyzed the pteridophyte flora in terms of four ecological zones, established on the basis of differences in vegetation physiognomy, elevation, and climate (see also Young & León 1988, 1990a). Note that we here subdivide the "montane forest zone" of Figure 1 into three altitudinally distinct zones. We have surveyed relatively large tracts of each of the four zones discussed here: the tropical alpine zone, ~25 km^2; the montane rain forest zone, ~5 km^2; the montane wet forest zone, ~20 km^2; and the lower montane wet forest zone, ~5 km^2.

THE PTERIDOPHYTES

A total of 174 pteridophyte species in 43 genera have been found in the Park (Tables 1-4). The two most speciose genera were *Elaphoglossum* with 28 species and *Grammitis* s.l. with 23. Other diverse groups included the lycopods, particularly *Huperzia*, 17 species; *Asplenium*, 10 species; *Hymenophyllum*, 9 species; and *Thelypteris*, 8 species.

Most of the species were recorded as terrestrial herbs (95 species, 55%) or epiphytes (36 species, 21%), or else were found in some situations growing terrestrially and in others epiphytically (30 species, 17%). Other growth form categories represented were tree ferns (5, 3%), climbers (2, 1%), aquatics (1, < 1%), or "not recorded" (4, 2%).

PTERIDOPHYTE HABITATS AND GROWTH FORMS

Tropical alpine zone

Approximately 22% of the area of Rio Abiseo National Park falls within the tropical alpine zone, known locally as "jalca" or "páramo" (Figures 1 and 2) and present from 3200-4200m. By far the most common vegetation type consisted of tussock grasslands dominated by species of *Calamogrostis, Cortaderia, Festuca* and *Stipa*. Within the matrix created by these tussocks grew approximately 250 species of vascular plants, including growth forms that ranged from cushion plants and acaulescent forbs to low-growing shrubs. Sixty-five pteridophyte species known from the upper elevations of the Park occurred here (Table 1). Twenty-three of these species were found only in this zone.

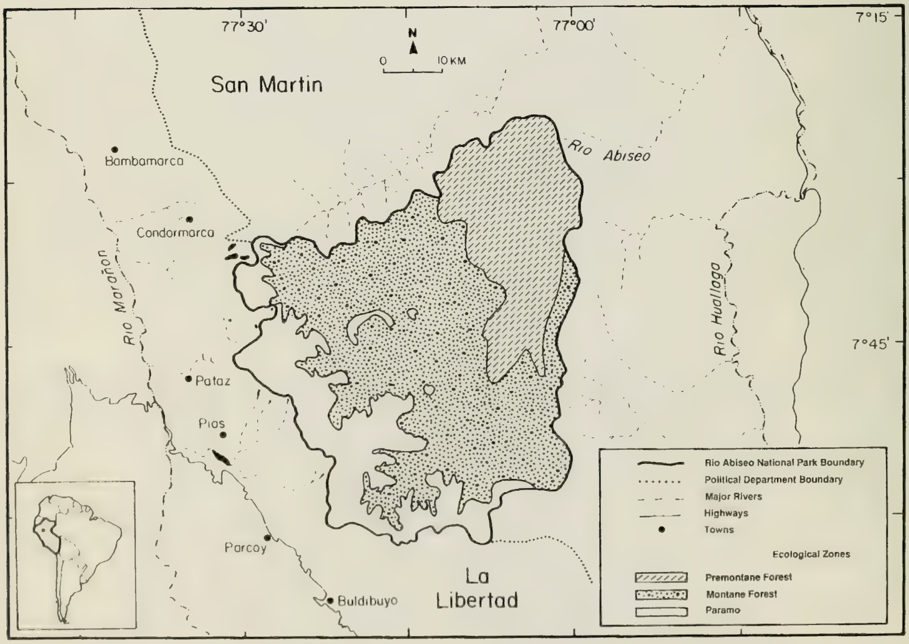

FIGURE 1. Map of Rio Abiseo National Park in north-central Peru.

Fire is not a natural disturbance in this zone: lightning occurs at the height of the rainy season and is almost always associated with heavy rainstorms. However, the grasslands have long been burned in order to improve grazing for cattle. When full control of the boundaries of this national park is achieved, it is expected that the cattle will be removed

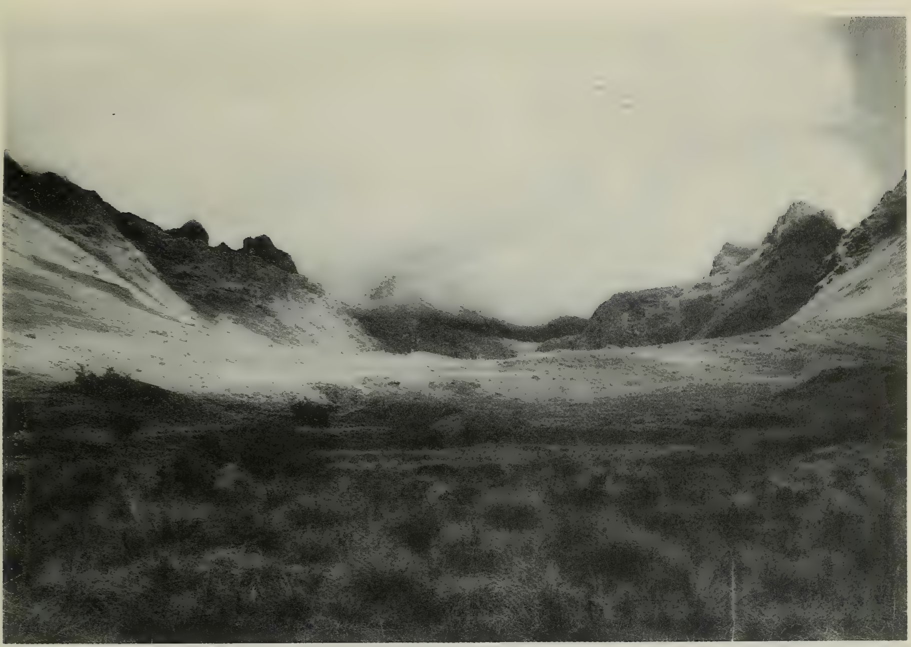

FIGURE 2. Photograph of tussock grasslands in the tropical alpine zone.

and burning will cease. Many of the pteridophytes most common in the grasslands appeared to be preadapted to fire by virtue of having subterranean rhizomes and the ability to resprout following defoliation. These included *Gleichenia simplex, Jamesonia alstonii, J. peruviana,* and *Lycopodium magellanicum.* Other possibilities included those used by *Ophioglossum crotalophoroides,* which resprouted from its underground tuber, and *Blechnum loxense,* which was protected by and resprouted from its thick stem.

A grassland habitat important for pteridophytes, but easily overlooked by pteridologists, was that doughnut-shaped zone between the base of a tussock grass and the outer circumference of its leaves. This shaded microenvironment is protected from climatic extremes, although probably not from severe fires. Species present included several ferns only found here (*Hymenophyllum multialatum, Grammitis rostrata,* and two as yet unidentified species of *Grammitis*) and several others that are also present as epiphytes (*Grammitis* sp.) or herbs (*Eriosorus rufescens*) in the forest.

The lycopods were conspicuous, although never dominant members of the tussock grasslands. It was possible to associate different ecological roles with each of the three genera present (Fig. 3; Øllgaard 1979, 1987). The two species of *Lycopodiella* were open-space occupiers, covering small areas of bare soil between tussocks with numerous, short-branching axes adpressed to the soil surface. Their fertile stems arose vertically from the axes, reaching 15cm in height. Few other plants could grow within the 25-100cm^2 areas occupied by a *Lycopodiella alopecuroides* clone; other plants present with similar tendencies were cushion plants: *Azorella* spp., *Plantago tubulosa, Xyris subulata.* In dense stands of tussock grasses, or in areas that have not burned recently, *Lycopodiella alopecuroides* was less frequent, presumably because it was not particularly shade tolerant.

The *Lycopodium* species were resilient opportunists, running distances of 2-3m with long, often partly buried axes. They resprout following fire, and send up vertical fertile stems often as tall as the surrounding graminoids. Of the three common species, *Lycopodium*

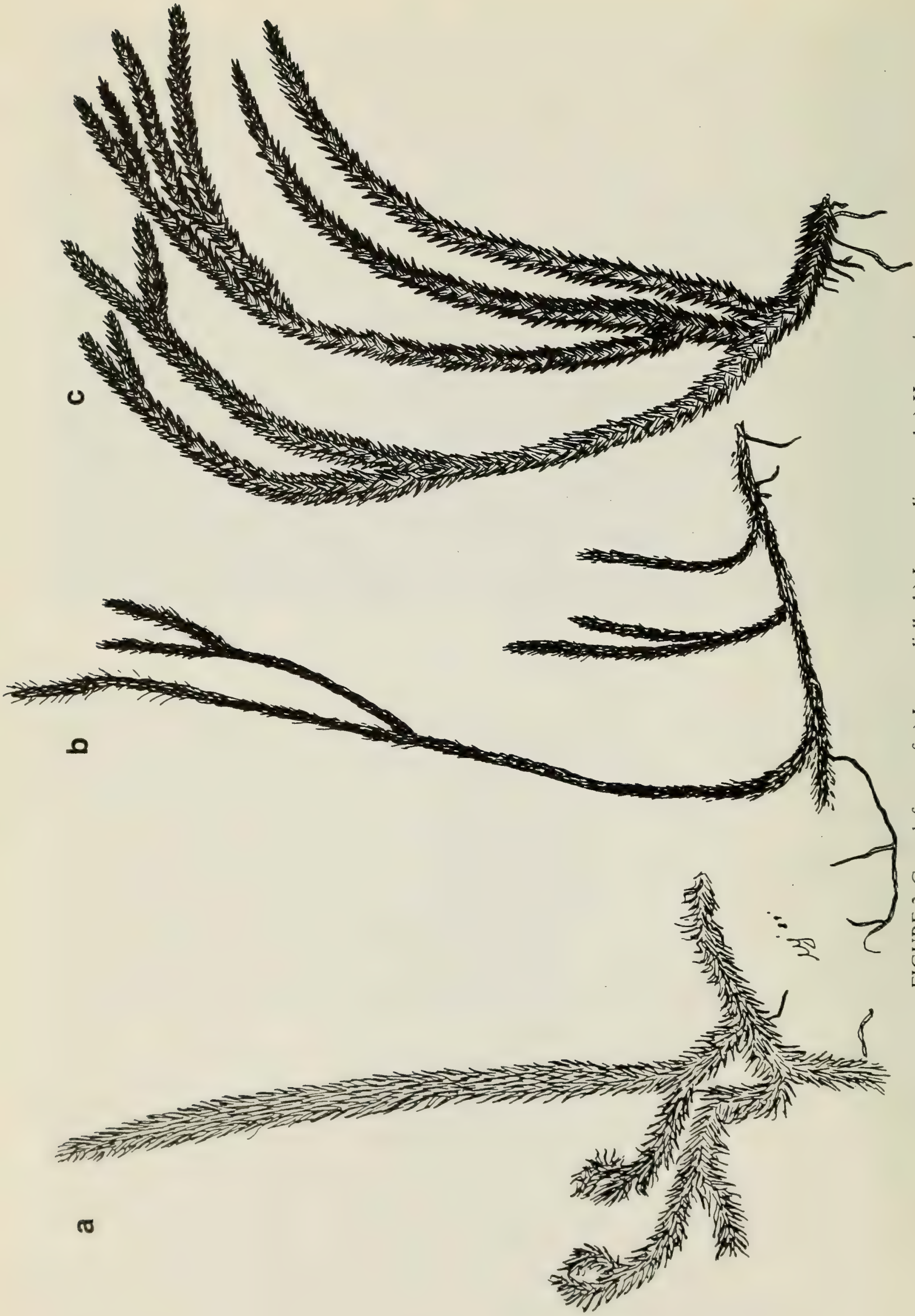

FIGURE 3. Growth forms of a) *Lycopodiella*, b) *Lycopodium*, and c) *Huperzia*.

magellanicum had the smallest fertile stems (5-15cm tall), with *L. clavatum* and *L. thyoides* both reaching 25cm heights, or more if they should clamber up the base of a tall tussock grass.

The seven species of *Huperzia* were harder to classify, except perhaps as more conservative in their growth patterns. All had a relatively short main axis (1-10cm long) pressed flat against the ground. The proximal portion of each axis was found dried and decomposing, while the distal portion, besides advancing horizontally along the ground, supported the several vertical or clambering fertile stems, which were 10-40cm long. *Huperzia ?macbridei macbridei, H. weberbaueri,* and *H. tetragona* were all common, with the last mentioned being a relatively short, erect species, while the former two species were longer and clambered up or grew amidst the graminoids.

Equisetum bogotense was frequently present in poorly drained areas of the grasslands. Also present, although inconspicuous, was a squat *Isoetes* sp.

Two other *Isoetes* species were present in the zone. These were aquatic or semiaquatic plants, apparently allopatric in distribution within the Park. For example, a lake at 3300m elevation (in Chochos valley) was dominated by a large, robust *Isoetes* sp., while the nearest other lake, 500m away and 50m higher in elevation, was dominated by a small, quite distinct *Isoetes* sp. Presumably chemical difference between the lakes might explain this distribution, although competitive exclusion is an interesting alternative.

A significant habitat for ferns was that provided by large boulders that are found isolated in the grasslands or in boulder fields under cliffs. These rocks offered a shaded microenvironment with protection from frost and wind. Equally or more significant perhaps was the fact that plants growing under the lips of boulders or in crevices around them were protected from fire, as there was little fuel there to carry the flame. Eleven fern species were restricted to this habitat, and several others were present there and also in other protected microsites (Table 1). None of these ferns displayed obvious morphological adaptations to climatic extremes. However, few other species of vascular plants were present, suggesting that shade tolerance and great diaspore mobility were adaptations that allowed ferns to preferentially exploit this habitat.

The four epipetric species (Table 1) were present on exposed surfaces of the boulders. These ferns had obvious morphological adaptations: reduced leaf size and coverings of hairs and/or scales.

Species found both out in the grasslands and inside the timberline forest showed a marked difference in size, with smaller, but thicker, leaves and pinnules in exposed individuals. Examples include *Lophosoria quadripinnata, Polystichum montevidense* and *Thelypteris caucaensis.* Eight of the nine *Elaphoglossum* species found to date in the tropical alpine zone (the exception being *E. engelii*) were also present inside the nearby timberline forest. Fertile grassland plants of these species were 50-75% smaller in size than those within the forest, often taking on sizes and shapes that resulted in the plants being sheltered under or near grass tussocks or boulders.

Montane rain forest zone

The uppermost belt of forest, located above 3100m elevation and reaching 3700m, consisted of montane rain forest, also known as mossy forest due to an abundance of epiphytic mosses, hepatics, and filmy ferns (Fig. 4). Much of the precipitation arrived in the form of mist, and fog was present 3 to 24 hours each day. Forest-interior trees generally reached 7-20m in height, and the understories were often dominated by one of several climbing bamboo species of the genus *Chusquea* (Young 1990). This zone harbored 109 of the species of pteridophytes (Table 2); 49 species were found only here, including 14 species of *Elaphoglossum*, and five each of *Huperzia, Hymenophyllum* and *Grammitis* s.l.

The boundary between the high elevation grasslands and the timberline portion of the montane rain forest was usually narrow and well defined. It had apparently been originally determined, and was currently maintained, by occasional fires that run through the grasses only to be stopped by continually moist conditions within the forest. Because of the resprouting of shrubby species and the exuberant growth of herbaceous and woody vines, this forest-edge habitat was dense and low. Pteridophytes found here included some species more typically encountered out in the grasslands (*Blechnum loxense, Eriosorus cheilanthoides, E. rufescens, Jamesonia imbricata, Lycopodium clavatum, L. thyoides, Polystichum montevidense*) and others that were essentially forest species (Table 2). *Hypolepis obtusata* appeared to be the only species restricted to this ecotone.

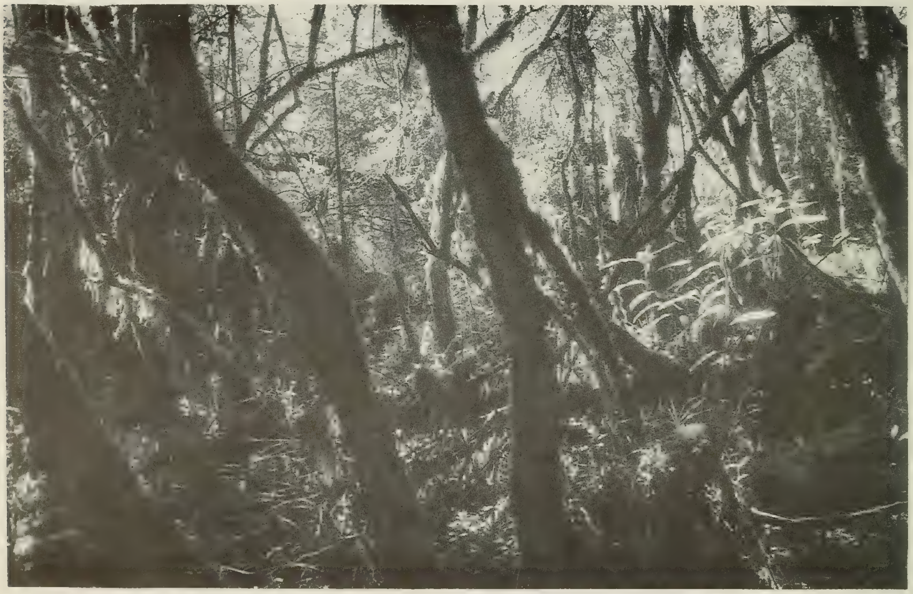

FIGURE 4. Photograph of the interior of the montane rain forest at 3450m.

A striking number (19 or 17%) of forest-interior pteridophyte species were found both as terrestrial herbs and as epiphytes (Table 2; includes two as-yet-undetermined *Elaphoglossum* spp.). In some cases these were herbs that had fortuitously germinated in the dense epiphytic mats covering large tree trunks and limbs; in others, normally epiphytic taxa had fallen to the forest floor and continued growth there.

The three common species of *Hymenophyllum* were generally epiphytes and occasionally could be found growing intertwined on the same tree. *H. fucoides* was a semi-erect filmy fern reaching 15cm in height and common from 3550m down to 3100m. Both *H. myriocarpum* and *H. plumieri* were pendent species 20-30cm long; the former was most abundant above 3400m, while the latter only occurred below that altitude.

Campyloneurum amphostenon and *C. ensifolium* were common, often sympatric, species growing on organic material on the forest floor, or else as epiphytes. The four *Polypodium* species in this zone were usually epiphytic, although *P. buchtienii* and especially *P.* cf. *eurybasis* could be found growing on the ground with some frequency. Four of the 17 *Grammitis* species (Table 2) were sometimes terrestrial but, by and large, species of this genus were epiphytes.

The most diverse genus in this zone, *Elaphoglossum* with 24 species, was largely composed of epiphytes, with an occasional individual found growing on the ground. Dimorphy between sterile and fertile leaves was frequent within this group. Three species (*E. minutum, E. ruficomus,* and an *Elaphoglossum* sp.), which occurred out in the grasslands, but also grew less commonly as epiphytes in the forest, had a particular form of dimorphy whereby the petiole of the fertile leaf was two or three times longer than those of the sterile leaves; the result was that spore production and release take place from an elevated position. However, the remaining forest species known from fertile material displayed a type of dimorphy perhaps more suited to spore presentation and release by an epiphyte: the fertile leaf's surface area was always smaller and its petiole often shorter than those of the sterile leaves. Moran (1987) also found that terrestrial species of *Polybotrya* had fertile-leaf petioles longer than sterile-leaf petioles and the epiphytic species had the reverse, although in all his examples the fertile leaf's surface area was smaller than the sterile leaf's.

The most impressive epiphytes were the relatively coarse *Huperzia molongensis* and the delicate *H. tenuis*, both of which reached 1m in length as they hung pendent from the undersides of large branches. Neither was common and individual plants grew on widely separated trees.

Three epipetric species have been observed here on boulders or rock exposures (Table 2), but none were common.

Wholly terrestrial pteridophytes in the forest interior were mostly components of the dense understory. Certain of these species had creeping rhizomes or flexible stems and could scramble up to a limited height or else can grow out from under fallen branches: *Blechnum kunthiana, Gleichenia rubiginosa, Histiopteris incisa, Huperzia hippuridea, H. rosenstockiana, Thelypteris brausei, T. caucaensis.* Others were likely to be fixed in one place, but had comparatively thick, erect stems that, besides in themselves providing some stature and protection to the plants, might serve for the storage of starches, thus allowing for the regrowth and replacement of damaged leaves; these species were *Athyrium dombeyi, Blechnum buchtienii, B. cordatum, Dryopteris wallichiana, Lophosoria quadripinnata* and *Plagiogyria semicordata.*

The three species of true tree ferns (Table 2) had massive stems that allowed them to reach well up into the subcanopy at 4-6m height. In some places more than a quarter of all plant stems $\geqslant$ 2.5cm diameter were of tree ferns (Young 1990).

Montane wet forest zone

Fog usually formed above 3100m; the zone of montane forest beneath this elevation still received plentiful precipitation, but almost always in the form of heavy rainstorms and with several weeks of dry season, usually in July and/or August. We recognize this as the montane wet forest zone with a lower elevational limit at about 2700m. This zone contained 61 species of pteridophytes (Table 3), 30 of which were only found here. This was a complex zone ecologically as it included rock outcrops and cliffs, extensive areas of steep (60-80°) slopes with numerous landslides, some forested areas with trees to 35m tall on gentler slopes, and a narrow but geomorphically active riverine zone (Fig. 5). Epiphytes were much less abundant than in the montane rain forest. Understories were always dense, dominated by the bamboo, *Chusquea scandens* Kunth, and shrubs of the genera *Miconia, Palicourea, Piper* and *Psychotria.*

Among the pteridophyte species recorded for this zone, 36% (22) were epiphytes or occasionally epiphytes, and many (68%) of these were uncommon (Table 3). The relative scarcity of *Hymenophyllum* spp. was symptomatic of being in a more seasonal environment. Only two pteridophyte species were observed growing epipetrically (Table 3).

Characteristic pteridophytes for this zone were instead the terrestrial species. In narrow elevational belts (from higher to lower elevation) the following species were conspicuous in the understory: *Cyrtomium dubium, Diplazium* spp., *Dennstaedtia globulifera, Selaginella asplundii, Pteris* spp. and *Elaphoglossum huacsaro.* Also present were four species of tree ferns (Table 3), although these were not as abundant as in the montane rain forest.

Asplenium was well represented here with seven species, four of which were commonly encountered (Table 3).

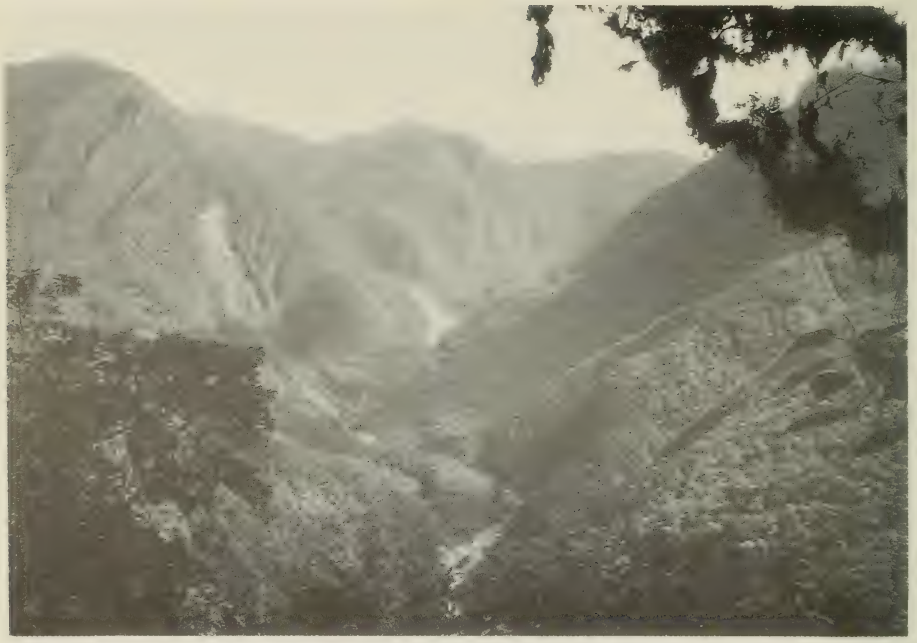

FIGURE 5. Photograph of the montane wet forest zone of Rio Abiseo National Park.

Two climbing ferns were present: *Blechnum kunthiana*, which was commonly seen, especially at approximately 3000m elevation, as an erect terrestrial herb and also as a trunk climber, reaching heights of 2-3m; and *Blechnum schomburgkii*, whose robust rhizome was observed once 2m up a tree trunk at 2700m.

The riverine vegetation shared numerous plant species with that found on recent landslides. Pteridophytes occupying these exposed sites were relatively few and inconspicuous: *Niphidium crassifolium*, *Pityrogramma calomelanos* and *P. tartarea*.

Lower montane wet forest zone

The transition from montane to lower montane forest at about 2700m was marked by the disappearance of the tree ferns and the common bamboo species, *Chusquea scandens*, and the appearance of palms (*Chamaedorea poeppigiana* Willd. and *Prestoea acuminata* (Willd.) Moore) and cyclanths (*Asplundia moritziana* (Klotsch) Hart., *Sphaeradenia steyermarkii* Hart.). Only 12 pteridophyte species have been recorded to date for this zone (Table 4), because of limited collecting. Five of these species have been found only in this zone.

ECOLOGICAL ZONATION

Similarity indices were used to compare the species lists of each ecological zone (Table 5). In general, these indices were low because relatively few species were shared between zones. Larger index values were always found between adjacent zones. The largest calculated were between the tropical alpine and montane rain forest zones, which shared 36 species, and between the montane rain forest and montane wet forest zones, which shared 28 species.

Genera found both in the tropical alpine zone and the spatially interdigited, montane rain forest zone were *Adiantum, Asplenium, Blechnum, Campyloneurum, Cystopteris, Elpahoglossum, Equisetum, Eriosorus, Gleichenia, Grammitis* s.l., *Huperzia, Hymenophyllum, Hypolepis, Jamesonia, Lophosoria, Lycopodium, Niphidium, Plagiogyria, Polypodium, Polystichum* and *Thelypteris*.

Genera found both in the montane rain forest zone and in the adjacent, but lower montane wet forest zone were *Antrophyum, Asplenium, Athyrium, Blechnum, Campyloneurum, Cyathea, Cyrtomium, Dryopteris, Elaphoglossum, Grammitis* s.l., *Huperzia, Hymenophyllum, Lophosoria, Lycopodium, Niphidium, Polypodium, Thelypteris, Trichipteris* and *Trichomanes.*

Most of the pteridophytes had narrow elevational ranges in the study area. Average elevational range for all 174 species was 264m (SD = 274). Relatively small elevational amplitude could be due to ecological specialization, but could also be a sampling artifact due to limited collecting of naturally sparse species. Thirteen species were represented by at least five separate collections, yet still showed elevational ranges of $\leq$ 200m. Of these, those that were limited to $\leq$ 150m ranges were *Blechnum loxense, Elaphoglossum rimbachii, Polystichum orbiculatum, Huperzia* sp., *Grammitis athyrioides* and *Jamesonia scalaris.*

In contrast, 16 species had elevational ranges $>$ 700m. These were mostly montane forest species, sometimes crossing over into the tropical alpine zone or also growing in the lower montane forest. Three species (*Niphidium crassifolium* s.l., *Polypodium buchtienii,* and *Thelypteris caucaensis*) were present in all four zones. The largest elevational ranges were those of *Polypodium buchtienii* (1300m), *Thelypteris concinna* (1300m), *Thelypteris caucaensis* (1250m) and *Polypodium* cf. *eurybasis* (1050m).

The average elevational range for all of the species found in each zone increased as altitude decreased: tropical alpine zone (258m (SD = 271)), montane rain forest (342m (SD = 300)), montane wet forest (425m (SD = 361)), lower montane wet forest (650m (SD = 527)). However, the only zones significantly different (at $p < 0.05$; paired Wilcoxon signed-rank tests) in mean elevational range were the tropical alpine and montane wet forest zones ($p < 0.001$).

TABLE 1:
Pteridophytes of the tropical alpine zone.

Species	**Observations**
Adiantum poiretii Wikstr.	only near boulders
Adiantum raddianum C. Presl	only near boulders
Asplenium monanthes L.	only near boulders
Asplenium triphyllum C. Presl	only near boulders
Blechnum buchtienii Rosenst.	only on forest edges
Blechnum cordatum (Desv.) Hieron.	only on forest edges
Blechnum loxense (HBK) Hieron.	usually near forest edges
Botrychium schaffneri Underw.	uncommon
Campyloneurum amphostenon (Klotzsch) Fée	uncommon, only near boulders
Campyloneurum ensifolium (Willd.) Fée	near boulders or epipetric
Cystopteris fragilis (L.) Bernh.	only near boulders
Elaphoglossum engelii (Karsten) Christ	sometimes near boulders
Elaphoglossum melancholicum Vareschi	uncommon
Elaphoglossum minutum (Fée) Moore	
Elaphoglossum odontolepis Mickel, nom. ined.	uncommon, only near boulders
Elaphoglossum petiolosum (Desv.) Moore	only near boulders
Elaphoglossum rimbachii (Sodiro) Christ	uncommon
Elaphoglossum ruficomus Mickel, nom. ined.	sometimes epipetric
Elaphoglossum spp.	two species
Equisetum bogotense HBK	
Eriosorus cheilanthoides (Sw.) A. Tryon	
Eriosorus rufescens (Fée) A. Tryon	only near grass tussocks
Gleichenia revoluta HBK	
Gleichenia rubiginosa Mett.	
Gleichenia simplex (Desv.) Hook.	
Grammitis moniliformis (Lag. ex Sw.) Proctor	sometimes epipetric
Grammitis rostrata (Hook.) R. Tryon & A. Tryon	

Grammitis spp.	four species
Huperzia columnaris B. Øllg. vel sp. aff.	
Huperzia ?macbridei (Herter) B. Øllg.	
Huperzia tetragona (Hook. & Grev.) Trevisan	
Huperzia weberbaueri (Nessel) Holub	
Huperzia spp.	three species
Hymenophyllum multialatum C. Morton	only near grass tussocks
Hymenophyllum myriocarpum Hook.	only near tussocks or boulders
Hypolepis obtusata (C. Presl) Hieron.	only on forest edges
Isoetes spp.	three species
Jamesonia alstonii A. Tryon	
Jamesonia imbricata (Sw.) Hook. & Grev.	sometimes near boulders
Jamesonia peruviana A. Tryon	sometimes near boulders or epipetric
Jamesonia aff. *peruviana* A. Tryon	uncommon
Jamesonia scalaris Kunze	
Lophosoria quadripinnata (Gmel.) C. Chr.	
Lycopodiella alopecuroides (L.) Cranfill s.l.	
Lycopodiella caroliniana L. s.l.	uncommon
Lycopodium clavatum L.	
Lycopodium jussiaei Poiret	uncommon
Lycopodium magellanicum (Palisot) Sw.	
Lycopodium thyoides Willd.	
Lycopodium vestitum Poiret	uncommon, only on forest edges
Niphidium crassifolium (L.) Lellinger s.l.	uncommon, only near boulders
Ophioglossum crotalophoroides Walt.	
Plagiogyria semicordata (C. Presl) Christ	only near boulders
Polypodium buchtienii Christ & Rosenst.	only near boulders
Polystichum montevidense (Spreng.) Rosenst.	
Polystichum orbiculatum (Desv.) Remy & Fée	only near boulders
Thelypteris caucaensis (Hieron.) Alston	near boulders or in other protected microsites

TABLE 2.
Pteridophytes of the montane rain forest zone

Species	**Observations**
Adiantum poiretii Wikstr.	uncommon, terrestrial
Antrophyum lineatum (Sw.) Kaulf.	uncommon, epiphyte
Asplenium cristatum Lam.	uncommon, terrestrial
Asplenium cuspidatum Lam.	terrestrial
Asplenium harpeodes Kunze	epiphytic or terrestrial
Asplenium monanthes L.	usually terrestrial
Asplenium serra Langsd. & Fisch.	terrestrial
Asplenium sessilifolium Desv.	usually terrestrial
Athyrium dombeyi Desv.	terrestrial, sometimes on forest edges
Blechnum buchtienii Rosenst.	terrestrial, sometimes on forest edges
Blechnum cordatum (Desv.) Hieron.	terrestrial, sometimes on forest edges
Blechnum kunthianum C. Chr.	uncommon, terrestrial
Blechnum loxense (HBK) Hieron.	terrestrial, on forest edges
Botrychium virginianum (L.) Sw.	uncommon, terrestrial
Campyloneurum amphostenon (Klotzsch) Fée	epiphytic or terrestrial
Campyloneurum ensifolium (Willd.) Fée	epiphytic or terrestrial
Culcita coniifolia (Hook.) Maxon	uncommon, terrestrial
Cyathea pallescens (Sodiro) Domin	tree fern
Cyrtomium dubium (Karsten) R. Tryon & A. Tryon	terrestrial
Cystopteris fragilis (L.) Bernh.	uncommon, terrestrial
Dryopteris wallichiana (Spreng.) Hyl.	terrestrial
Elaphoglossum albescens (Sodiro) Christ	epiphytic or terrestrial
Elaphoglossum atrosquamatum Mickel	uncommon
Elaphoglossum barbatum (Karsten) Hieron.	uncommon, epiphytic
Elaphoglossum camptolepis Mickel, nom. ined.	uncommon, terrestrial

Elaphoglossum castaneum (Baker) Diels	uncommon
Elaphoglossum dichroum Mickel, nom. ined.	uncommon, epiphytic
Elaphoglossum erinaceum (Fée) Moore	*epiphytic*
Elaphoglossum glossophyllum Hieron.	uncommon
Elaphoglossum laxisquama Mickel, nom. ined.	epiphytic or terrestrial
Elaphoglossum melancholicum Vareschi	often epiphytic
Elaphoglossum minutum (Fée) Moore	terrestrial
Elaphoglossum odontolepis Mickel, nom. ined.	epiphytic
Elaphoglossum oxyglossum Mickel, nom. ined.	epiphytic
Elaphoglossum pachyphyllum (Kunze) C. Chr.	epiphytic or terrestrial
Elaphoglossum paleaceum (Hook. & Grev.) Sledge	epiphytic
Elaphoglossum petiolosum (Desv.) Moore	epiphytic or terrestrial
Elaphoglossum pilosius Mickel	uncommon
Elaphoglossum rimbachii (Sodiro) Christ	epiphytic or terrestrial
Elaphoglossum ruficomus Mickel, nom. ined.	epiphytic
Elaphoglossum squamipes (Hook.) Moore	epiphytic or terrestrial
Elaphoglossum vulcanicum Christ	epiphytic
Elaphoglossum spp.	3 species
Equisetum bogotense HBK	terrestrial
Eriosorus accrescens A. Tryon	terrestrial, usually on forest edges
Eriosorus cheilanthoides (Sw.) A. Tryon	terrestrial, usually on forest edges
Eriosorus rufescens (Fée) A. Tryon	epiphytic or terrestrial
Gleichenia rubiginosa Mett.	uncommon, terrestrial
Grammitis amylacea (Copel.) C. Morton	uncommon, epiphytic
Grammitis athyrioides (Hook.) C. Morton	pendent epiphyte
Grammitis ?cultrata (Willd.) Proctor	uncommon, pendent epiphyte
Grammitis ?firma (J. Sm.) C. Morton	epiphytic or terrestrial
Grammitis lanigera (Desv.) C. Morton	pendent epiphyte, rarely terrestrial
Grammitis pseudonutans (Christ & Rosenst.) C. Morton	epiphytic
Grammitis rigescens (Bory ex Willd.) Lell. vel sp. aff.	epiphytic, occasionally terrestrial
Grammitis semihirsuta (Klotzsch) C. Morton	epiphytic
Grammitis serrrulata (Sw.) Sw.	uncommon, epiphytic
Grammitis spp.	eight species, five uncommon; all epiphytic with one occasionally terrestrial
Histiopteris incisa (Thunb.) J. Sm.	uncommon, terrestrial
Huperzia arcuata B. Øllg.	uncommon, terrestrial
Huperzia eversa (Poiret) B. Øllg.	uncommon, terrestrial, on forest edges
Huperzia hippuridea (Christ) Holub	terrestrial
Huperzia molongensis (Herter) Holub	pendent epiphyte
Huperzia rosenstockiana (Herter) Holub	usually terrestrial
Huperzia subulata (Poiret) Holub	uncommon, epipetric
Huperzia tenuis (Willd.) Trevisan	pendent epiphyte
Huperzia weberbaueri (Nessel) Holub	uncommon, terrestrial
Hymenophyllum amabile C. Morton	uncommon, pendent epiphyte
Hymenophyllum elegantulum Bosch	uncommon, epipetric
Hymenophyllum fragile (Hedwig) C. Morton	uncommon, epiphytic
Hymenophyllum fucoides (Sw.) Sw.	epiphytic or terrestrial
Hymenophyllum myriocarpum Hook.	pendent epiphyte or terrestrial
Hymenophyllum plumieri Hook. & Grev.	pendent epiphyte or terrestrial
Hymenophyllum trichophyllum HBK	uncommon, terrestrial
Hypolepis obtusata (C. Presl) Hieron.	terrestrial, only on forest edges
Jamesonia imbricata (Sw.) Hook. & Grev.	terrestrial, often on forest edges
Lophosoria quadripinnata (Gmel.) C. Chr.	terrestrial, sometimes on forest edges
Lycopodium clavatum L.	terrestrial, usually on forest edges
Lycopodium jussiaei Poiret	terrestrial, usually on forest edges
Lycopodium thyoides Willd.	terrestrial, usually on forest edges
Lycopodium vestitum Poiret	terrestrial, only on forest edges
Niphidium crassifolium (L.) Lellinger s.l.	uncommon, epiphytic or terrestrial
Plagiogyria semicordata (C. Presl) Christ	terrestrial, sometimes on forest edges
Polypodium buchtienii Christ & Rosenst.	epiphytic or terrestrial
Polypodium cf. *eurybasis* C. Chr.	epiphytic or terrestrial

Polypodium spp.	two uncommon species, both epiphytic
Polystichum montevidense (Spreng.) Rosenst.	terrestrial, often on forest edges
Polystichum orbiculatum (Desv.) Remy & Fée	terrestrial, only on forest edges
Pteris deflexa Link	uncommon, terrestrial
Selaginella ?calosticha Spring	uncommon, epiphytic or terrestrial
Sphaeropteris atahuallpa R. Tryon	tree fern
Thelypteris brachypus (Sod.) A.R. Smith	uncommon, terrestrial
Thelypteris brausei (Hieron.) Alston	terrestrial, occasionally on forest edges
Thelypteris caucaensis (Hieron.) Alston	terrestrial, often on forest edges
Thelypteris concinna (Willd.) Ching	uncommon, terrestrial
Thelypteris funckii (Mett.) Alston	uncommon, terrestrial
Trichipteris frigida (Karsten) R. Tryon	tree fern
Trichomanes lucens Sw.	uncommon, pendent epiphyte
Vittaria ruiziana Fée	epiphytic, epipetric

TABLE 3.
Pteridophytes of the montane wet forest zone

Species	**Observations**
Antrophyum lineatum (Sw.) Kaulf.	uncommon, epiphytic
Arachniodes denticulata (Sw.) Ching	uncommon, terrestrial
Asplenium cuspidatum Lam.	epiphytic or terrestrial
Asplenium harpeodes Kunze	epiphytic or terrestrial
Asplenium hastatum Kunze	terrestrial
Asplenium serra Langsd. & Fisch.	terrestrial
Asplenium sessifolium Desv.	uncommon, terrestrial
Asplenium squamosum L.	uncommon, terrestrial
Athyrium dombeyi Desv.	uncommon, terrestrial
Blechnum cordatum (Desv.) Hieron.	uncommon, terrestrial
Blechnum kunthianum C. Chr.	terrestrial or climbing
Blechnum schomburgkii (Klotzsch) C. Chr.	uncommon, climbing
Campyloneurum amphostenon (Klotzsch) Fée	terrestrial
Campyloneurum angustifolium (Sw.) Fée	uncommon, epiphytic
Cyathea caracasana (Klotzsch) Domin	tree fern
Cyathea pallescens (Sodiro) Domin	tree fern
Cyathea sp.	uncommon, tree fern
Cyrtomium dubium (Karsten) R. Tryon & A. Tryon	terrestrial
Dennstaedtia globuligera (Poiret) Hieron.	terrestrial
Diplazium hians Klotzsch	terrestrial
Diplazium remotum Fée	terrestrial
Dryopteris wallichiana (Spreng.) Hyl.	uncommon, terrestrial
Elaphoglossum barbatum (Karsten) Hieron.	uncommon, epiphytic or terrestrial
Elaphoglossum concinnum Mickel, nom. ined.	uncommon, epiphytic
Elaphoglossum huacsaro (Ruiz Lopez) Christ	terrestrial
Elaphoglossum pachyphyllum (Kunze) C. Chr.	epiphytic or terrestrial
Elaphoglossum papillosum (Baker) Christ	uncommon, terrestrial
Equisetum giganteum L.	uncommon, terrestrial
Grammitis ?cultrata (Willd.) Proctor	epiphytic
Grammitis pseudonutans (Christ & Rosenst.) C. Morton	uncommon, epiphytic
Grammitis semihirsuta (Klotzsch) C. Morton	uncommon, epiphytic
Grammitis sp.	uncommon, epipetric
Huperzia arcuata B. Øllg.	*uncommon, terrestrial*
Huperzia cuneifolia (Hieron.) Holub	uncommon, pendent epiphyte
Huperzia rosenstockiana (Herter) Holub	uncommon, terrestrial
Huperzia wilsonii (Underw. & Lloyd) B. Øllg.	uncommon, terrestrial
Huperzia sp.	uncommon, pendent epiphyte
Hymenophyllum plumiere Hook & Grev.	uncommon, pendent epiphyte
Hymenophyllum polyanthos (Sw.) Sw.	uncommon, epiphyte
Lophosoria quadripinnata (Gmel.) C. Chr.	uncommon, terrestrial
Lycopodiella glaucescens (C. Pressl) B. Øllg.	uncommon, terrestrial

Lycopodium thyoides Willd.	uncommon, terrestrial
Megalastrum pulverulentum (Poiret) A.R. Smith & Moran	terrestrial
Niphidium crassifolium (L.) Lell. s.l.	epiphytic or terrestrial, in open sites
Pityrogramma calomelanos (L.) Link	uncommon, on landslides
Pityrogramma tartarea (Cav.) Maxon	uncommon, on river cobble
Polypodium buchtienii Christ & Rosenst.	epiphytic or terrestrial
Polypodium cf. *eurybasis* C. Chr.	uncommon, terrestrial
Polypodium fraxinifolium Jacq.	uncommon, epiphytic
Polypodium sp.	epiphytic
Pteris muricata Hook.	terrestrial
Pteris podophylla Sw.	terrestrial
Selaginella asplundii Crabbe & Jermy	terrestrial
Thelypteris caucaensis (Hieron.) Alston	uncommon, terrestrial
Thelypteris concinna (Willd.) Ching	terrestrial
Thelypteris (subgenus *Steiropteris*) sp.	uncommon, terrestrial
Thelypteris sp.	uncommon, terrestrial
Trichipteris frigida (Karsten) R. Tryon	tree fern
Trichomanes diaphanum HBK	uncommon, epiphytic
Trichomanes lucens Sw.	uncommon, pendent epiphyte or epipetric
Vittaria gardneriana Fée	uncommon, epiphytic

TABLE 4.
Pteridophytes of the lower montane wet forest zone

Species	**Observations**
Asplenium extensum Fée	terrestrial
Asplenium harpeodes Kunze	epiphytic or terrestrial
Asplenium hastatum Kunze	terrestrial
Campyloneurum pascoense R. Tryon & A. Tryon	terrestrial
Campyloneurum repens (Aublet) C. Presl	epiphytic
Dennstaedtia dissecta (Sw.) T. Moore	terrestrial
Niphidium crassifolium (L.) Lellinger s.l.	uncommon, epiphytic or terrestrial
Polypodium buchtienii Christ & Rosenst.	uncommon, terrestrial
Polypodium cf. *eurybasis* C. Chr.	uncommon, terrestrial
Thelypteris caucaensis (Hieron.) Alston	uncommon, terrestrial
Thelypteris concinna (Willd.) Ching	terrestrial
Thelypteris sp.	terrestrial

TABLE 5.
Similarity indices among the four ecological zones of the study area. Sorenson's Index = (2a/(2a + b + c)) × 100; Jaccard's Index = (a/(a + b + c)) × 100; where a = number of species shared between two zones, b and c = number of unique species in each respective zone; Mueller-Dombois and Ellenberg 1974.

Sorenson's

	tropical alpine	montane rain	montane wet
montane rain	41		
montane wet	11	35	
lower montane	8	10	19

Jaccard's

	tropical alpine	montane rain	montane wet
montane rain	26		
montane wet	6	21	
lower montane	4	5	11

CONCLUSIONS

Important pteridophyte habitat types for the tropical alpine zone included ameliorated microenvironments created by structural features such as boulders and grass tussocks. Pteridophytes might have advantages in colonizing (and recolonizing) such sites because of the relatively high dispersability of spores. In addition, the size, spatial patterning, and composition of the tussock grasslands and their pteridophyte flora, were affected by topography, drainage and fire history (Young & León, unpublished data). Generally, pteridophytes in the grasslands either resprouted following fire, or were unaffected by it because they grew in protected microsites. We suggest that the role of fire must be considered for virtually all high-elevation, tropical Andean grasslands, even those in which fire would not occur without human assistance.

The forest zones were not as easily subdivided into discrete pteridophyte habitat types and those we noted mostly paralleled the growth form categories used. Near timberline, in the highest elevation forest, here called montane rain forest, there was a blurring of distinctions between epiphytic and terrestrial pteridophytes because of the presence of 5-20cm of organic matter on the forest floor (Young & León 1990b) and the formation of 0.5-3cm of soil underneath the exuberant plant growth on the tree trunks and major limbs (described also by Gill (1969) for Puerto Rican montane forests). Terrestrial pteridophytes appeared to recover from small-scale forest disturbances caused by tree-and branchfall by either resisting such disturbance with thick stems and the replacement of damaged leaves, or by recovery using a creeping or climbing stem. Cliffs, boulders, or other rock exposures did offer a specialized habitat to a small number of pteridophytes. In the montane wet forest zone, landslides and a dynamic riverine habitat shared many plant species, including a depauperate pteridophyte flora.

There was great individuality among pteridophyte species in elevational ranges and ecological zonation. Stevens (1989) developed a proposal by Rapaport (1982) into a generalization he called "Rapaport's rule" whereby there is a simple positive correlation between the latitudinal extent of the distribution of species plotted against latitude. We found some evidence in this study that for pteridophytes this relationship may be reversed when elevational rather than latitudinal ranges are considered. That is, the mean elevational amplitude of pteridophyte species tended to increase at successively lower zones in the Park. The tropical alpine pteridophytes, on average, showed less elevational amplitude than those composing the montane wet forest pteridophyte flora.

The montane rain forest zone, located at 3100-3700m, was by far the most species-rich zone, even though size of area sampled was one of the smallest. This is at odds with one of the major generalizations of Gentry (1982, 1988) that plant species diversity decreases with increases in altitude from 1500 to 3000m in the Andes; this demonstrates the importance of considering pteridophytes in assessments of plant diversity gradients. León & Valencia (1988) found 87% of their 23 pteridophyte species in the highest ecological zone sampled, a montane moist forest at 2700-3200m in the Peruvian Andes.

Why were there so many pteridophyte species near timberline in our study area? It apparently was not a sampling artifact because much larger areas were surveyed in the tropical alpine and montane wet forest zones, although further exploration needs to be done, especially in the ecologically diverse and often inaccessible montane wet forest zone from 2700-3100m. One reason for the high diversity is clearly that the montane rain forest zone shares many species respectively with both of its neighbouring ecological zones. The timberline forest has a low and occasionally open canopy that in some sites allows much light to reach the forest floor, but probably still provides a more moderated climatic regime than would be expected out in the grasslands. Another explanation might center on the fact that in the montane rain forest zone both substrate and humidity conditions allow normally terrestrial or epiphytic species to grow in the opposite state. Yet another reason would be the notable diversity present of certain pteridophyte groups, especially *Elaphoglossum*, in cool, continuously humid Andean forests. Because of the similar findings of León & Valencia (1988), we suggest that for these reasons high elevation cloud forests in the Andes are likely to have the most pteridophyte species.

Human impact in the upper part of Rio Abiseo National Park is mostly limited to occasional burning of the tussock grasslands. If this area were traversed by a road, it is likely that our data on habitat and elevational amplitudes would have been very different. A road that goes from high to low elevations in tropical montane areas creates a corridor for the upward and downward movements of forest-edge species, road-cut species, and of those growing in successional vegetation in logged forests or on abandoned agricultural fields. For example, at the elevations sampled in this study, but along a road or highway, we would expect bracken fern, *Pteridium aquilinum* (L.) Kuhn, to be present, if not dominant. Studies based on roadside collections of pteridophytes would probably demonstrate greater relative abundance of epipetric species, of scrambling growth forms, and of those spreading aggressively by rhizome. Such studies also probably would document much greater elevational ranges for a less speciose pteridophyte flora. For these reasons, it is important that data also be considered from large intact wilderness areas where plants appear to be growing under conditions similar to those in which they evolved.

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VOLUME 14 PART 1 **1991**

CONTENTS

Page

MAIN ARTICLES

Variation in *Equisetum variegatum* (Equisetaceae : Pteridophyta)
- *Gavin Stark* 1

Fern Rusts in Mid-Wales and The Conjuror of Chalgrave
- *Raymond G. Woods* 5

***Dryopteris x furadensis* (Dryopteridaceae: Pteridophyta)**
a new endemic fern hybrid from Madeira
- *H. Wilfried Bennert, Helga Rasbach & Kurt Rasbach & Ronald L.L. Viane* 7

***Isoetes x hickeyi* (Isoetaceae: Pteridophyta)** in Canada
- *Daniel F. Brunton & Donald M. Britton* 17

Diversity, ecology and distribution of high-elevation pteridophytes within Rio Abiseo National Park, north-central Peru
- *Kenneth R. Young & Blanca Leon* 25

CORRIGENDA 16, 24

NOTES FOR CONTRIBUTORS, ETC. 40

REVIEW 23

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CURL-TIP DISEASE OF *PTERIDIUM AQUILINUM* (DENNSTAEDTIACEAE: PTERIDOPHYTA)

J.A. IRVINE [1], M. McELWEE [2] and M.N. BURGE [3]
Department of Bioscience & Biotechnology, University of Strathclyde
The Todd Centre, Glasgow G4 0NR

[1] Present address: Department of Botany and Microbiology,
University College, London, Gower Street, London WC1E 6BT

[2] Present address: Department of Botany, University of Glasgow,
Glasgow, G12

[3] To whom correspondence should be addressed.

ABSTRACT

Field observations and laboratory investigations have elucidated the symptoms, aetiology and disease cycle of curl-tip of bracken, *Pteridium aquilinum.* Two Coelomycete fungi are involved: *Ascochyta pteridis* is the primary invader attacking the host directly, whereas *Phoma aquilina* is a common secondary invader of damaged tissue. The potential of these fungi as biological control agents is discussed.

INTRODUCTION

Outbreaks of the disease of bracken *(Pteridium aquilinum* (L) Kuhn) known as curl-tip have been reported in the U.K. on several occasions (Alcock & Braid, 1928; Braid, 1934; Angus, 1958; Burge & Irvine, 1985.

The severity of the disease, which occurs on open hill-land where control of bracken is most desirable, strongly suggests that the pathogen(s) responsible would provide the active ingredient(s) for a mycoherbicidal formulation. Our work towards this goal is presented elsewhere (Burge & Irvine, 1985; Burge *et al.,* 1986; Irvine *et al.,* 1987; McElwee et al., 1990; Munyaradzi *et al.,* 1990). An integral part of this work involves an understanding of the biology of curl-tip disease and the purpose of the present paper is to review the current knowledge of the aetiology and cycle of the disease.

CURL-TIP DISEASE

Occurrence

In the first report of curl-tip disease, Alcock and Braid (1928) noted twenty sightings of outbreaks of curl-tip in Scotland, and concluded that it occurred over "the whole of Scotland south of a line through Loch Rannoch". Angus (1958) examined outbreaks at two further Scottish sites. An additional twenty-six sightings in the U.K. were reported by Burge & Irvine (1985), extending from Inverness in the north to the Isle of Wight in the south. The disease also occurs in California, where it has been studied by Webb & Lindow (1986) as a potential biological control agent.

Symptoms

The mature symptoms of curl-tip have been reported on several occasions (Alcock & Braid, 1928; Barnett, 1931; Braid, 1934, 1947, Angus, 1958; Burge & Irvine, 1985; Irvine *et al,* 1987). Burge & Irvine (1985) and Irvine *et al.* (1987) observed the first signs of disease as numerous brown spots, typically 0.5mm in diameter clustered together near the bases of the young emerging fronds (Fig. 1). These spots gradually elongated and coalesced to give rise to more extensive, sunken, necrotic lesions which occasionally extended from base to apex of the frond (Fig. 2). Other observations agreed with those of earlier workers in that fronds could be attacked at all stages of their development; young croziers failed to

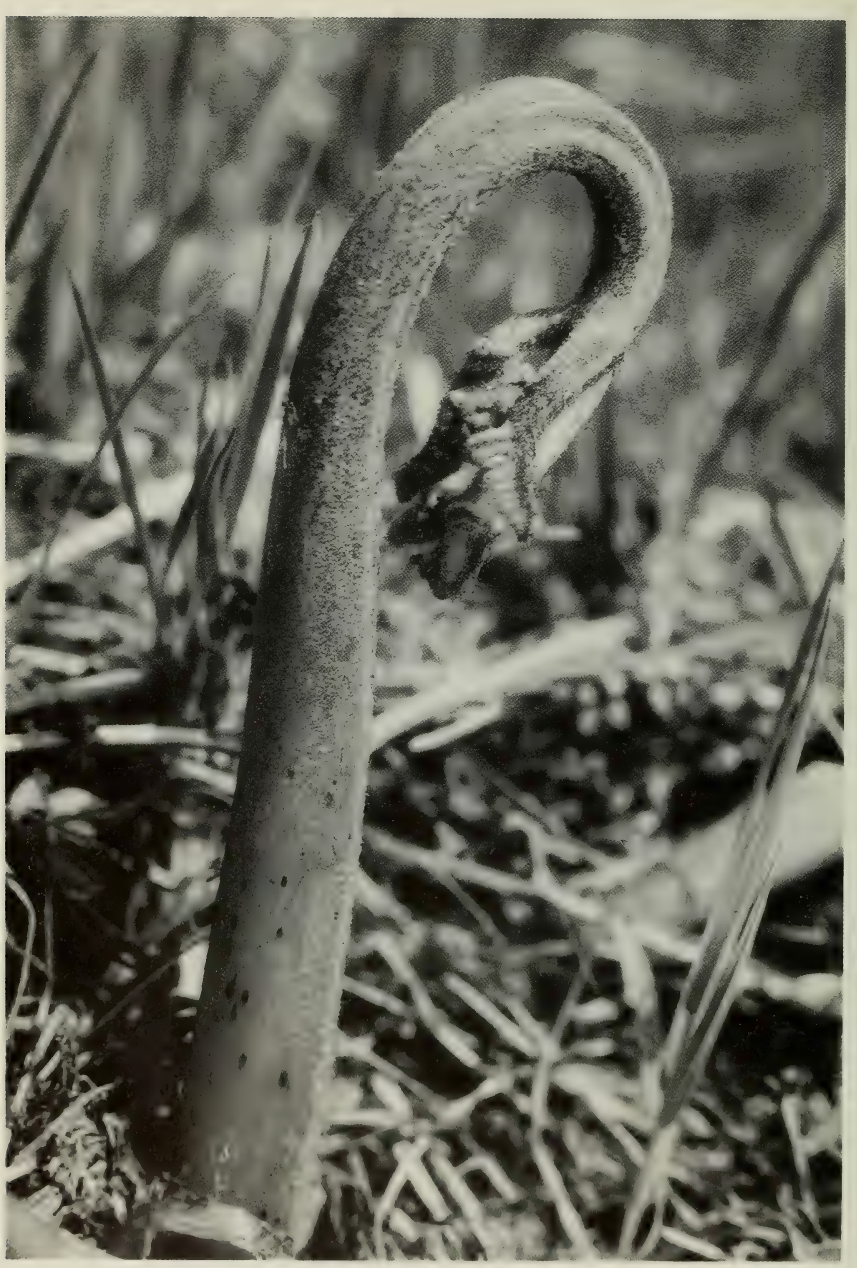

FIGURE 1. The first visible symptoms of the curl-tip syndrome: spotting on emergent croziers caused by *Ascochyta pteridis*.

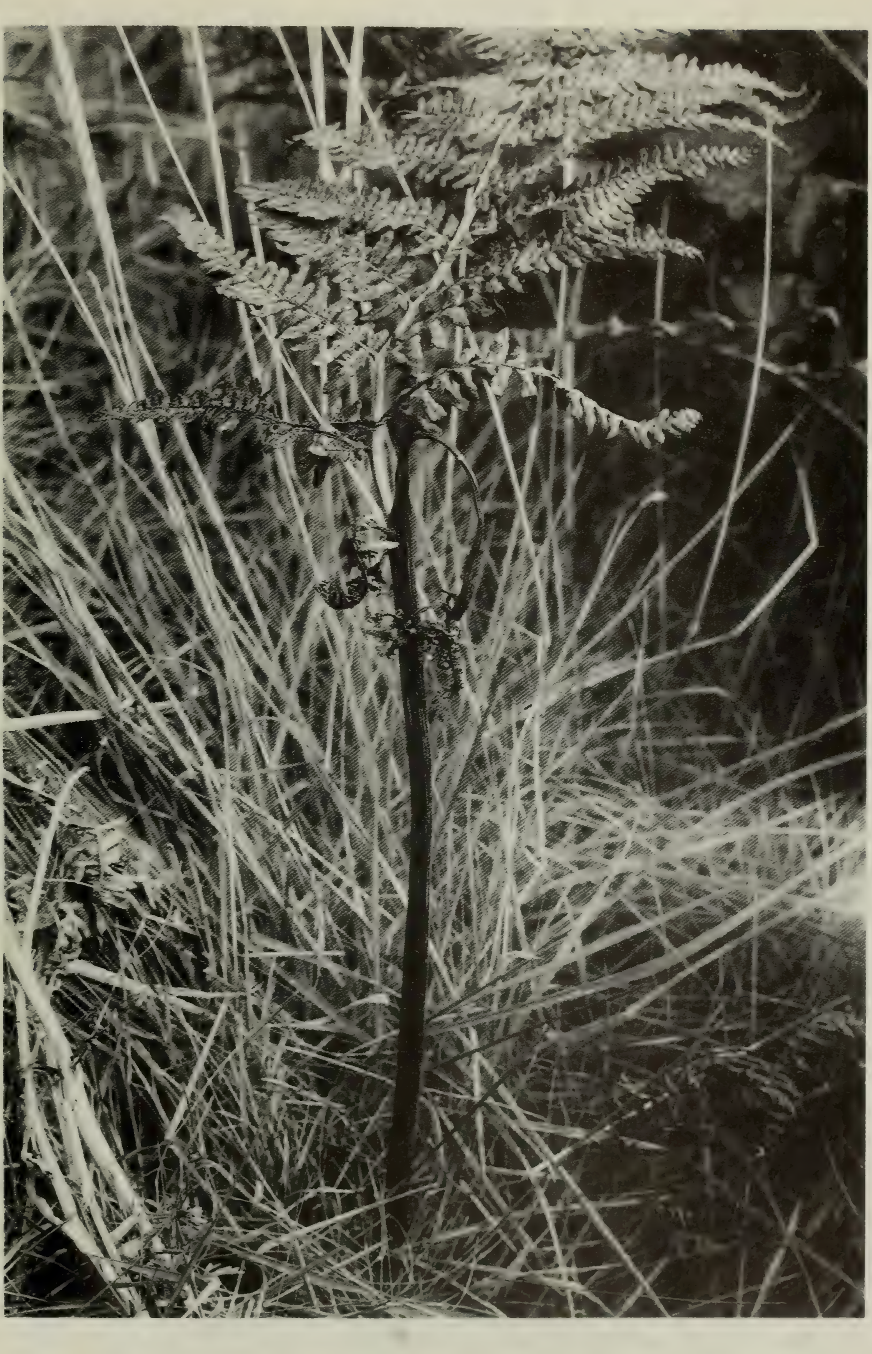

FIGURE 2. Extensive brown necrosis of stipe and characteristic curled apex.

unfurl, became discoloured, shrivelled and died. Older infected fronds often became twisted and lop-sided due to lack of development of some of the lateral pinnae, and their apices became characteristically curled and necrotic (Fig. 2).

In contrast to dense stands of healthy bracken which often totally eliminate other plants from the same habitat, stands of diseased bracken are considerably thinned and the underlying flora develops vigorously, facilitating grazing by stock which in turn may exacerbate the damage. Assessment of natural disease development in ungrazed plots at West Linton in 1982 indicated that the number of fronds with necrotic, curled tips increased from 3% in mid-June, to 66% by mid-August. A comparison of bracken cover between diseased and nearby non-diseased sites in mid-August indicatd a 60% reduction of cover in the diseased area, although it must be recognised that other factors may be involved (Irvine, unpublished data).

Fungal isolates

Braid (1934) noted the presence of fungal "pustules" on necrotic tissue, but no isolates were obtained in pure culture. Angus (1958) isolated three pycnidial fungi from curl-tip diseased bracken: *Ascochyta pteridis* Bres., *Phoma aquilina* Sacc. and Penz. and a *Stagonospora* spp. Burge & Irvine (1985) also consistently isolated *A. pteridis* and *P. aquilina* as well as a *Septoria* sp. which is possibly the same as Angus' *Stagonospora*. Reisolation from the smallest spot lesions on young croziers consistently yields *A. pteridis* colonies, indicating that it is the primary pathogen (Burge *et al.*, 1986). As these lesions begin to enlarge, platings yield *P. aquilina* as well as *A. pteridis* suggesting that the former is a weaker pathogen lacking the ability to attack the host directly. *Stagonospora* was commonly reisolated from well developed lesions; on one occasion, during wet weather, numerous spore tendrils of this fungus were visible to the unaided eye. Occasionally, diseased bracken has been found, but close examination and enquiry have revealed that other agents such as herbicides, drought, frost or even diesel spillage has been the cause. However, attempts to isolate pathogens from such material invariably yield plentiful *P. aquilina* colonies, providing further evidence (q.v.) that this fungus is an opportunistic necrotroph with only weak pathogenicity to undamaged bracken.

Proof of pathogenicity

Angus (1958) reported the infection and death of greenhouse-grown bracken inoculated with spores of *Phoma aquilina*. Numerous trials have failed to confirm these results (Irvine, unpublished data). However, curl-tip symptoms could be induced when rachises were wound-inoculated with portions of spore-bearing colonies of *P. acquilina* from malt extract agar. It was also found that applications of spores of *A. pteridis* (but not *P. aquilina*) to the rachises of young greenhouse-grown bracken resulted in spot symptoms, but not the full curl-tip syndrome. Development of these lesions progressed when the spots were over-sprayed with spores of *P. aquilina*, and typical curl-tip symptoms developed. However, comparison of the effects of inocula containing spores of each fungus independently or in combination, indicated that the presence of *P. aquilina* significantly reduced the amount of damage caused by *A. pteridis* alone. The *Stagonospora* isolate failed to induce disease whatever the inoculation method, suggesting that this fungus may be a saprophyte favouring the micro-habitat created by the other two fungi (Irvine *et al.*, 1987).

Penetration and Invasion

Light and scanning electron microscopy of pinnule and petiolar epidermal strips of naturally and experimentally inoculated tissue reveals that stomata are commonly exploited for penetration by *A. pteridis* (Fig. 3), whereas direct penetration by *P. aquilina* has not been observed. Although clear evidence of complete penetration through epidermal cell walls by either fungus has not yet been obtained, there is a microscopically visible reaction in epidermal cell walls in the vicinity of the inoculum of both fungi. These are conspicuous hemispherical ingrowths (papillae) which develop on the inner wall surfaces and staining indicates that they are comprised of an inner lignified core and an outer cover of callose (Fig. 4). The cell walls themselves also become lignified. Germ tubes are often seen in direct assocation with papillae, suggesting the involvement of the latter in the resistance response (McElwee & Burge, 1990). Further evidence for direct epidermal penetration is obtained from the fact that necrotic symptoms develop on pinnae which have been inoculated on their adaxial surfaces where stomata are absent. Damage is more severe when the inoculum is applied to the abaxial surface where stomata are abundant.

Light microscopy of transverse sections of moribund tissue shows mycelium in the cortex and xylem. The fact that both fungi move systemically beyond the region of inoculation and necrosis development has been demonstrated by reisolation of the pathogens from symptom-free, surface-sterilised frond segments several centimetres above and below the focus of wound inoculations (Irvine, unpublished data). Details of the invasive process have yet to be determined.

Reproduction

Colonies of *A. pteridis* and *P. aquilina* on solid or liquid media such as malt extract or potato dextrose readily produce large numbers of pycnidia from which spores are released. Pycnidia are formed on artifically or naturally inoculated bracken as soon as necrosis occurs. Sections of moribund tissue reveal pycnidia of both fungi, often in close association. In wet weather, spore tendrils can be seen on the surface of such tissue. In naturally diseased sties, pycnidia also occur in abundance on lesions in bracken litter, suggesting that the fungi overwinter in this state. When moistened, these litter-borne pycnidia release large quantities of spores, indicating that in such sites the litter harbours a large reservoir of inoculum to infect young emergent croziers (Irvine *et al.*, 1987).

The disease cycle is summarised diagrammatically in Fig. 5.

Potential for biological control with the curl-tip pathogens

Bracken is one of the world's most widely distributed and troublesome weeds (Page, 1976; 1982). Taylor (1986) concluded that bracken covers some 6,720 Km^2 of the U.K. and that the average rate of encroachment in England and Wales alone is 1% per annum, rising to 3% in some areas.

As well as aggressive invasion of valuable hill pasture, the ingestion of bracken by sheep, cattle, horses or pigs causes a variety of toxic and carcinogenic effects (Evans, 1976, 1986). The possibility that the carcinogenic properties may affect man is perhaps remote but must not be ignored. Bracken is consumed as a delicacy in some areas, especially Japan, where stomach cancer is prevalent (Hirono *et al.*, 1972). It may be also be indirectly consumed *via* milk (Evans, I.A. *et al.*, 1972) or ground water (Galpin & Smith, 1986) or by the inhalation of spores (Evans, 1986). Bracken also harbours a large reservoir of ticks which cause ailments to sheep (Milne, 1950) and grouse (Hudson, 1986).

Clearly, control of bracken is necessary. A major problem in this context is the enormous resource of the tough rhizome system bearing large numbers of buds from which new fronds are rapidly regenerated. Mechanical control is labour-intensive and largely ineffective. Systemic chemicals such as asulam destroy the rhizome buds resulting in effective control (Veerasekaren *et al.*, 1976) but are used infrequently for reasons of cost effectiveness. There is thus a need for an alternative method of control. The general prospects for the biological control of bracken with insects or fungi have been discussed elsewhere (Burge *et al.*, 1988).

There is increasing interest in the use of indigenous fungal plant pathogens of weeds formulated as biological control agents known as mycoherbicides (Charudattan, 1989). There are, however, few fungal pathogens that cause significant damage to bracken. The rust fungi *Uredinopsis hashiokai* and *U. pteridis* which cause perennial needle rust of firs complete

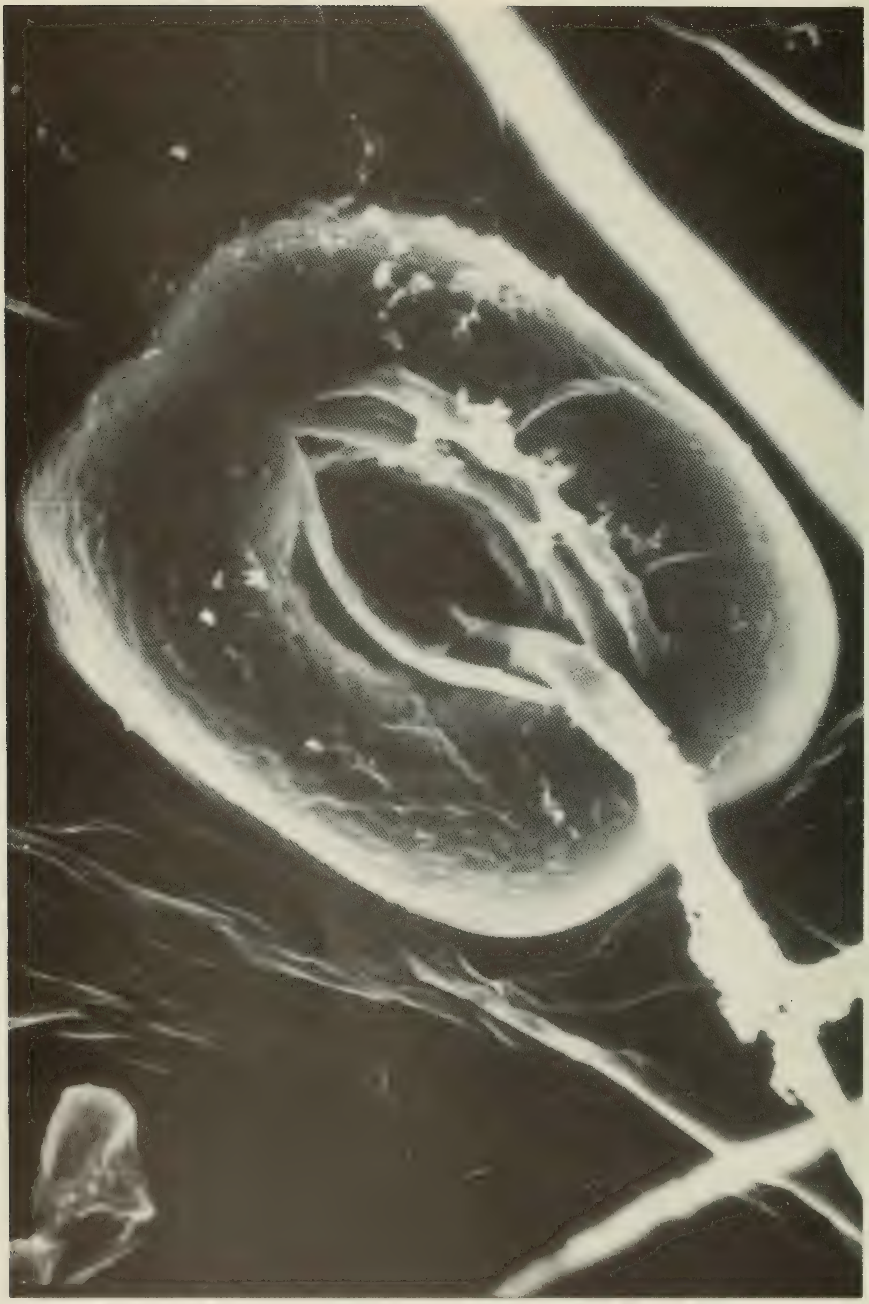

FIGURE 3. Germ tube of *Ascochyta pteridis* penetrating stomatal pore.

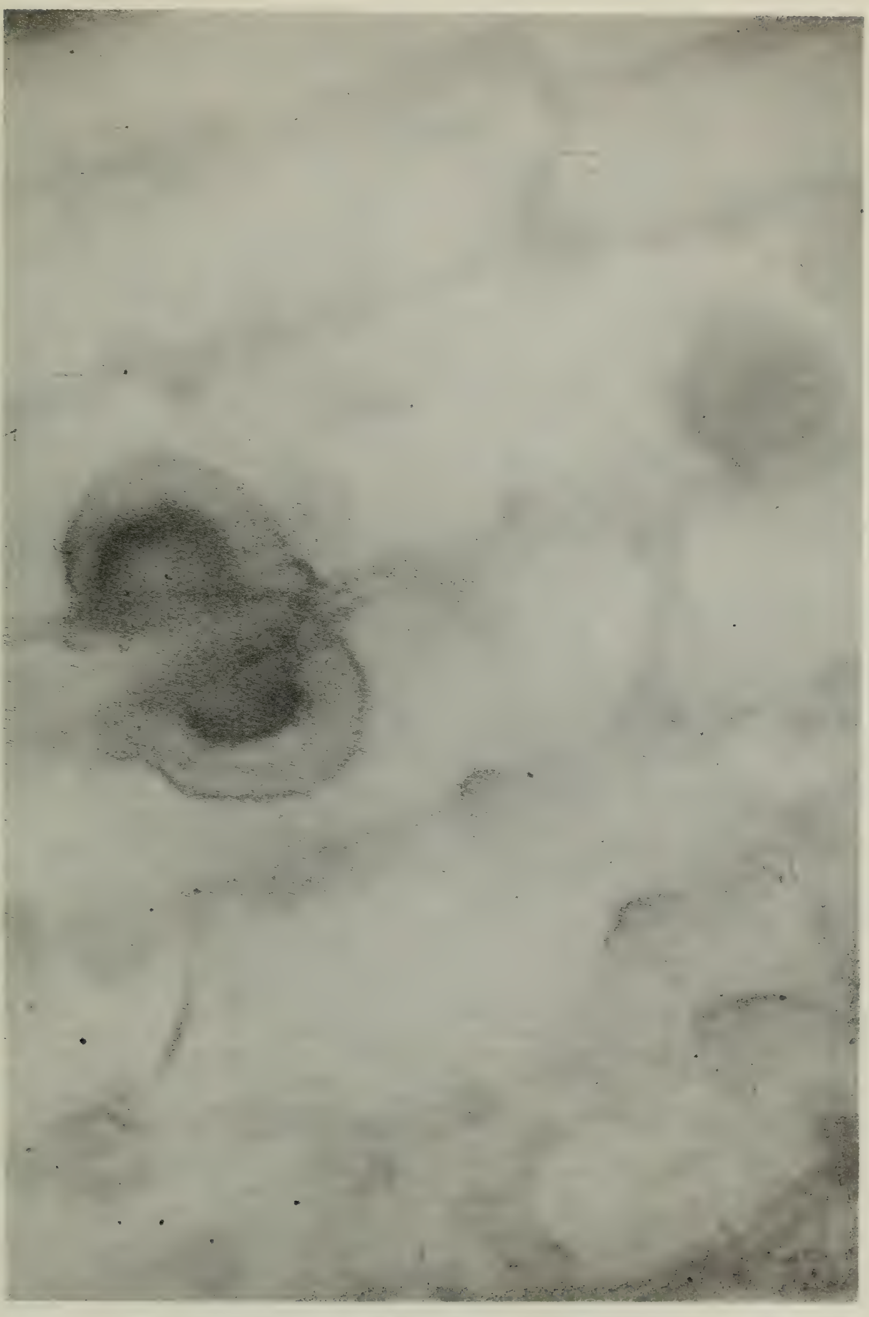

FIGURE 4. Papillae on epidermal cell walls. Note outer cover of callose and inner lignified core.

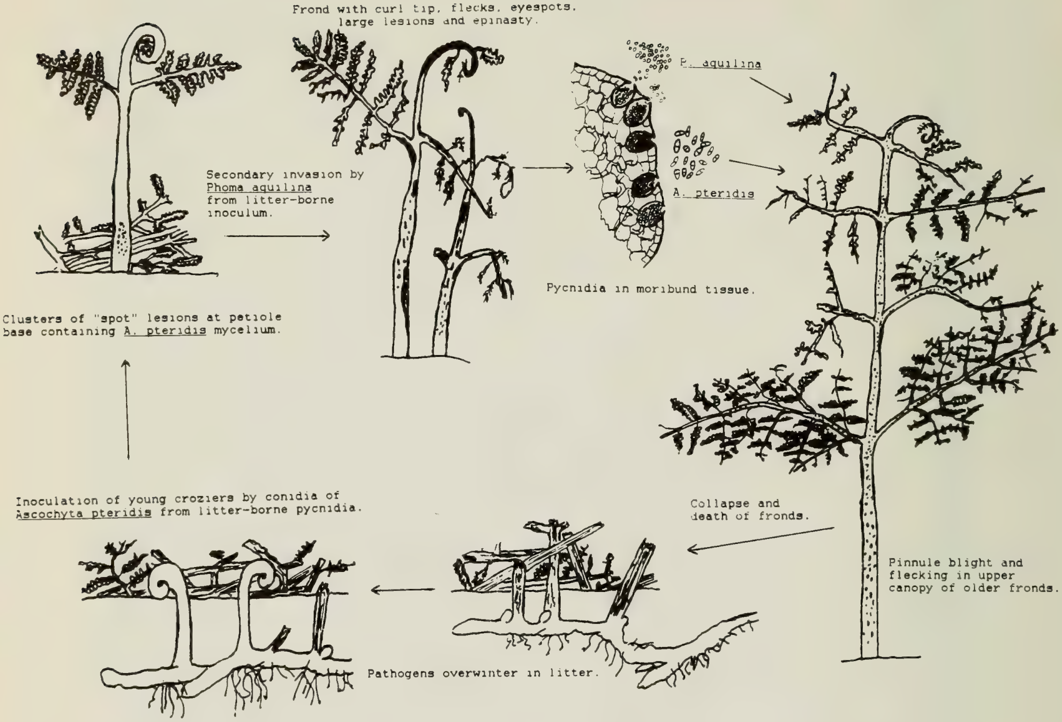
Frond with curl tip, flecks, eyespots, large lesions and epinasty.
P. aquilina
A. pteridis
Secondary invasion by Phoma aquilina from litter-borne inoculum.
Pycnidia in moribund tissue.
Clusters of "spot" lesions at petiole base containing A. pteridis mycelium.
Inoculation of young croziers by conidia of Ascochyta pteridis from litter-borne pycnidia.
Collapse and death of fronds.
Pinnule blight and flecking in upper canopy of older fronds.
Pathogens overwinter in litter.

FIGURE 5. The disease cycle of bracken curl-tip.

their life cycles on bracken (Ziller, 1959); *Ceratobasidium anceps* causes blight of pinnae in woodland situations (Gregor, 1935) and *Cryptomyces pteridis* causesd a systemic infection resulting in leaf-roll (Bache-Wiig. 1940). For several reasons, none of these fungi is considered to be a suitable candidate for biological control of bracken in the U.K. However, the curl-tip pathogens, in particular *A. pteridis*, have potential in that they are capable of attacking bracken in open moorland habitats; they produce spores abundantly in simple culture media; they are indigenous to the U.K. and have never been recorded on any host other than bracken. The major draw-back is that pathogenicity is relatively low, except under certain environmental conditions. For this reason our work continues to examine the potential of a range of adjuvants to the inoculum which enhance pathogenicity in a variety of ways (Munyaradzi *et al.*, 1990). Studies on the biology of the disease will continue to be a necessary component of this work.

ACKNOWLEDGEMENTS

We are grateful to the DAFS, AFRC and MAFF for providing financial support.

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SHORT NOTE

THE MALESIAN PTERIDOPHYTES OF RACIBORSKI

The Javanese Pteridophyta collected by Marian Raciborski housed in the Herbarium of the Jagiellonian University (KRA) has been discussed – Zesz. Nauk. Uniw. Jagiellońskiego, Prace Bot. 18 (1989), pp, 127-133. The article contains some information on the nomenclatural types of Raciborski's Pteridophyta, an itinerary of the collection, and a map showing most of the localities from which the pteridological specimens of this collection originated. The author would like to announce that an alphabetical list (in typescript) of Raciborski's Malesian pteridophytes has recently been prepared, and is available in the library of the Jagiellonian University Botanical Institute (ul. Lubicz 46, 31-512 Kraḱow, Poland).

P.S. KÖHLER
Hortus Botanicus Univ. Jagellonicae, Kraków, Kopernika 27, Poland

REVIEWS

SOUTH AFRICAN FERNS AND FERN ALLIES by J.E. Burrows (illustrations by S.M. Burrows) c.432 pp, 56 colour plates (comprising 330 photographs), 22 habitat photographs, 300 distribution maps, over 800 line-drawings, 297 x 210 mm (11¾ x 8¼ inches). July 1990. ISBN 0-620-14616-8, Frandsen Ltd, P.O. Box 122, Fourways 2055, South Africa. Price £63.

Southern Africa as defined in this book includes South Africa, Namibia, Botswana, Zimbabwe and Mozambique, is delimited on the north by the Cunene, Karango and Zambesi Rivers which form a convenient east-west boundary across the continent, and extending south to the Cape. Climate varies from warm temperature to tropical, differences being accentuated by several mountainous areas rising to over 3000 m and the presence of extensive deserts in the interior. The region supports an interesting and varied pteridophyte flora, and 343 species are described in this book. This represents only 3.5% of the world total, because there is only a comparatively small area of forest, and true rain forest is absent; many species are adapted to semi-arid conditions. In the Palaeozoic period when the region was part of the ancient continent of Gondwanaland the ancestors of present-day groups of pteridophytes were abundant, but lycopods and ferns suffered almost complete extinction at the end of the period some 250 million years ago, and the lycopods have never recovered. Horsetails continued to be abundant for another 50 million years, and then declined rapidly. Ferns diversified and increased, reaching the peak of their abundance between 160 and 100 million years ago, since when they have declined again. These variations over vast periods of time affect the composition of the extant flora, which does not only depend on present-day conditions.

The author, who was born forty years ago in Zimbabwe, formerly worked at the Kirstenbosch Botanic Garden, Cape Town, and is now curator of a nature reserve near Lydenburg in the Transvaal. He commenced working on this Flora in 1980, and since then has travelled all over the region photographing the plants in their natural habitats. Throughout he has been accompanied by his wife, also formerly employed at Kirstenbosch who prepared the more than 800 line drawings that illustrate the book. Modern knowledge of the pteridophytes of the region began in 1892 with T. R. Sim's *The ferns of South Africa* (second revised edition, 1915). Since then it has been greatly extended by the researches of E. A. C. L. E. Schelpe, who contributed (posthumously) the account of pteridophytes in the *Flora of Southern Africa* (1986). W. B. G. Jacobsen published *The fern and fern*

continued on page 54

ALLELOPATHY IN BRACKEN *PTERIDIUM AQUILINUM* (DENNSTAEDTIACEAE: PTERIDOPHYTA)

I. N. JOSEPHINE STOREY
North House, Hayes Road, Bromley, Kent BR2 9AF, England

ABSTRACT
The allelopathic effects of bracken *Pteridium aquilinum* on nine plant species were simulated by the application of four phenolic acids (p-coumaric, ferulic, p-hydroxybenzoic, vanillic) under laboratory conditions, to study the effects of bracken on other plant species.

Bracken *Pteridium aquilinum* (L.) Kuhn is now known to be toxic, both to Man and to other animals (Cooper & Johnson, 1984; Fenwick, 1989) and there has been much research on the possible link between bracken and human gastric cancer. Bracken may also be toxic to other plants and even to itself. Pliny claimed that the best way to kill bracken was to knock off its 'stalk' with a stick when it was 'budding' "as the juice trickling down out of the fern itself kills the roots" (Rice, 1984). The degeneration of old stands of bracken after a number of years may be a symptom of autotoxicity (Harborne, 1988). What about bracken's toxicity to other plants? Could this be a factor in its increasing ecological success?

The ecological success of bracken is now recognised to be a problem (eg: Taylor, 1980; Smith & Taylor, 1986) for its known and possible effects on animals and Man, and for its competition with crops and other beneficial plants (eg: Cooper & Johnson, 1984; Evans, I.A., 1984; Perring & Gardiner, 1976; Page, 1986). Glass (1976) found that barley plants grown hydroponically in solutions which exactly reproduced the major phenolic acid composition of the soil associated with bracken (as measured by Whitehead, 1964) exhibited inhibited root growth in O.5mM calcium sulphate solution. Glass's 1976 paper formed the basis for some studies I carried out as a part-time student at Birkbeck College, University of London (Storey, 1990) to investigate the effects of the phenolic acids (in particular at soil concentrations) on wild plants found in the same habitat as bracken, to compare these effects with those of bracken itself (frond and rhizome leachates) and to look for differences in response between species and relate these differences to their ecology, in particular to their possible inhibition by bracken frond leachate. The effect investigated was a possible allelopathic interaction contributing to the ecological success of bracken. The term allelopathy is derived from the Greek "allelon" meaning 'of each other' and "pathos" 'to suffer' – the injurious effect of one upon another. It was coined by Molisch in 1937 (Bhushan Mandava, 1985). Rice (1987) indicated that the term was intended to refer to biochemical interactions between all types of plants, including microoganisms traditionally placed in the plant kingdom. Molisch's discussion indicated that he meant the term to cover both inhibitory and stimulatory biochemical interactions. The general subject of allelopathy is reviewed in Rice, 1984; Thompson, 1985 and Waller, 1987.

According to Bhushan Mandava (1985) phenolic acids are components of the largest group of secondary plant products, often referred to as "phenolics" and identified as allelopathic agents in more instances than all of the other classes of compounds combined. The four phenolic acids used in my investigations were vanillic acid, p-coumaric acid, p-hydroxybenzoic acid and ferulic acid. Two of these, vanillic and p-hydroxybenzoic acids, are benzoic acids and two, p-coumaric and ferulic acids, are cinnamic acids. Benzoic and vanillic acids are present in leaf leachates and are known to have allelopathic activity. Cinnamic and coumaric acids are widely distributed in the plant kingdom and reported to be allelopathic chemicals.

I studied the effect of these four phenolics on nine native plant species, all but one grasses, to see if the effect of this simulated bracken leachate on the plants grown hydroponically in the laboratory could be related to their distribution relative to bracken in the field. The grasses used were Cocksfoot *(Dactylis glomerata* L.), Tufted Hair-Grass *(Deschampsia caespitosa* (L) Beauv.), Wavy Hair-Grass *(Deschampsia flexuosa* (L.) Trin.), Fine-Leaved Sheep's Fescue *(Festuca filiformis* Pourret, synonym *F. tenuifolia* Sibth.), Sheep's Fescue *(Festuca ovina* L.), Meadow Fescue *(Festuca pratensis* Hudson), Perennial Rye-Grass *(Lolium perenne* L.) and Annual Meadow-Grass *(Poa annua* L.). The one non-grass was Wood Sage *(Teucrium scorodonia* L.). Brief field studies were carried out on Hayes Common, Kent and the proximity of some of these species to bracken was compared with the effect of phenolic solution in the laboratory on root growth. There was some suggestion from the results that the species least-affected by phenolic solution in the laboratory grew nearest to bracken in the field and vice versa. In the laboratory root extension was inhibited by the phenolic solution and roots could develop what I would describe as a 'gelatinous' appearance as a mucilage-like material appeared around them. This would disappear as the concentration of phenolics fell and may have been a defensive response to poisoning. Perennial Rye-Grass was the most-affected species and Wavy Hair-Grass the least affected. Wavy Hair-Grass is often found growing near bracken. It is slow-growing, shade-tolerant, has low nutrient requirements and is found on acid soils (Hackett, 1967; Mahmoud & Grime, 1974). Were it not for competition from other species the grass would grow best in fertile soils of intermediate pH (Rorison, 1969). Perennial Rye-Grass, by contrast, is a grass of fertile soils, absent from highly acidic soils.

The phenolics used are known to interfere with nutrient uptake by plant roots, particularly under acidic conditions (eg: Glass, 1973; Glass, 1974; Glass & Dunlop, 1974). These phenolics are certainly not unique to bracken but they concentrate beneath the fern as bracken litter builds up. I suggest that, on nutrient-poor, acidic soils, bracken may inhibit the growth of neighbouring plants by interfering with their ability to take up nutrients from the soil. Plants with low nutrient requirements, such as Wavy Hair-Grass, would be most resistant and able to grow closest to bracken, though other factors (eg: shade tolerance) would also be involved.

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REVIEWS

continued from page 50

allies of southern Africa (the first popular illustrated account) in 1983. Burrows' book is a most worthy successor to these.

The accounts of all the 343 species (twelve of which are not native, but which have been introduced) include nomenclatural details (author, type-specimen, synonyms, derivation of name) and a full description. The latter includes excellent full page black-and-white drawings (on one page, showing four species of Adiantaceae in which the fronds are covered with silvery or golden scales, they are coloured). Attention is drawn to similar species. There is a paragraph on distribution, accompanied by a dot map. Of great value and interest is the further paragraph entitled ecology and notes which consists mostly of first hand field observations. The author believes that a preliminary step in identification can readily be made by reference to the colour photographs that are provided of every species, followed by consulting the drawings. The photographs, which are certainly all of a high quality, are grouped together at the beginning. Therefore he gives no keys to families and genera, though these are clearly indicated, and usually follow Schelpe. Within each genus there is a key to species, however.

As well as the systematic part of the book there are other interesting sections. The chapter on fern habitats distinguishes 24 types grouped as Mountains (5), Rocky Hills (2), Forests (10), Woodlands (2), Grasslands (3) and Deserts (2). A colour photograph of each and a list of typical ferns is provided. The Mountains include, of course, the Cape and its unique fynbos vegetation in which is to be found a number of pteridophytes found elsewhere in the South Atlantic oceanic islands; and even the deserts (the Karoo and the fringe of the Namib) support a few xerophytic ferns. There is also a list of common (English and Afrikaans) names; there are not very many of these, and they are often ambiguous. The author says "it cannot be stressed too strongly that the use of common names is no substitute for [using] the correct botanical name". Another remark from his useful introduction on how to use the book that is worth quoting is as follows: "Remember that many ferns are protected by law, and permission . . . must be sought before collecting . . . Even once this has been granted, remember that many of our ferns are very rare, with their habitats dwindling daily, and we therefore have a moral obligation to consider [their] survival". The book ends with an illustrated glossary, bibliography and index.

The outstanding feature of this work is the number and quality of the illustrations. But as is indicated above, it has other excellent qualities, and it is a most welcome pteridophyte Flora of an interesting and important part of the world.

F.H. BRIGHTMAN

PROCEEDINGS OF THE INTERNATIONAL SYMPOSIUM ON SYSTEMATIC PTERIDOLOGY edited by K.H. Sing & K.U. Kramer. 330 pp. 1989. ISBN 7-5046-0151-9/Q.5. China Science and Technology Press, Beijing.

This is the published papers of the Symposium held in Beijing on 5-10 September 1988, nicely presented as a hard-bound volume. It has been edited with care and attention to detail by Kramer and Shing. The original idea for a Symposium in China was born in 1978 when the reviewer was able to visit Professor R.C. Ching, eminent pteridologist and 'grand old man' of Chinese botany. The timing of the meeting was to celebrate Ching's 90th birthday, but alas he passed away in July 1986. As preparations were well advanced the Symposium commemorated his life and work and this volume opens with a review of Ching's contribution by another nonagenarian, R.E. Holttum; and K.H. Shing, long-time student of Ching and his successor in Beijing, reviews pteridological research in China – past and present.

continued on page 72

ANOGRAMMA LEPTOPHYLLA (SINOPTERIDACEAE: PTERIDOPHYTA) AN ANEUPLOID TAXON?

F. J. PÉREZ CARRO & Mª P. FERNÁNDEZ ARECES
C/ Caminante 8-2º B 24008- Leon, Spain

ABSTRACT

The variation in basic chromosome number reported for *Anogramma leptophylla* (L.) Link may be explained by the presence of B chromosomes or the larger size of a few chomosomes.

INTRODUCTION

Rasbach & Reichestein (1990) have recently considered that the exact chromosome number of *Anogramma leptophylla* (L.) Link is n= 26 II. This number agrees with the data of Gibby (1986: 120) and Queirós et al. (1988: 125) among others.

On the other hand, two other counts give a very different result, these being the studies made by Baroutsis & Gastony (1978) and Manton et al. (1986). These authors, directly or in their commentaries, suggest a possible aneuploid character for this taxon. These counts are n= 29 II (South African material) and n= c. 27±1 (material from Madeira) respectively. Moreover, these authors point out a certain ambiguity in the counts, mainly due to the characteristics of two of the chromosomic elements and also because of the sticky and glutinous character.

RESULTS AND DISCUSSION

Our observations, carried out on eighteen spore mother cells in meiosis of two adjacent individuals, could be considered as corroborating the results of Gibby (1986), Queirós et al. (1988) and Rasbach & Reichstein (1990) among the most recent authors. However there is another possible interpretation that can be given to the contents of these cells. This results from the observation of the contents of a single cell. In this cell (see Fig. 1: 1.1 and 1.1') 23 II and 3 complex formations are present, consisting of a bivalent of normal size and a chromosome element of a reduced size (outlined in the explanatory diagram 1.1'). The perfect configuration of the cell and its easy observation, do not seem to indicate that these elements result from the staining or squashing technique.

This observation is accompanied by a second, in the rest of the cells analysed. In them at least 2 II, sometimes 3, have a larger size (see outlined chromosomes Fig. 1: 1.2' and 1.3'). Similarly, examining the figures indicated by Rasbach & Reichstein (1990: 346), we could also identify the larger size of some bivalents. Until further evidence is obtained, we can suggest only that variation in chromosome size, possibly accompanied by the presence of B chromosomes may have contributed to the variation in chromosome counts for *Anogramma leptophylla*.

The material analysed (León: La Vid, town 2 km from Vegacervera, 30TTN85, 1300 m alt., *F. J. Pérez Carro & Mª P. Fernández Areces*, 1-V-89, PC-FA) grows at a higher altitude than is usual for this species.

ACKNOWLEDGEMENTS

We express our gratitude to Aurora Alonso.

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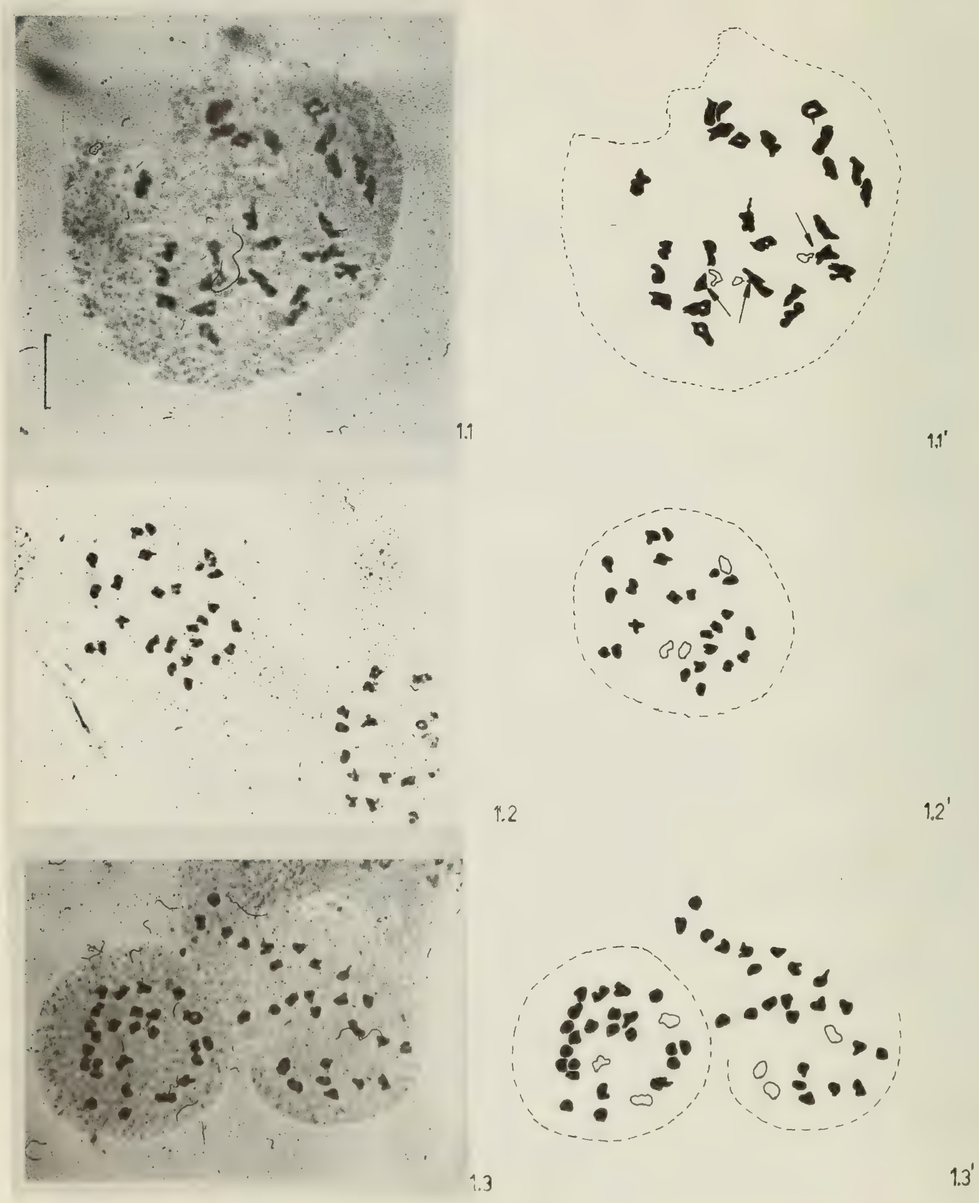

FIGURE 1: 1.1, 1.2 and 1.3= photographs (Bar = 10µm), 1.1', 1.2' and 1.3' = explanatory diagrams of spore mother cells in meiosis of *Anogramma leptophylla*: 1.1 and 1.1'= in diakinesis showing n= 26 II+ 3B, [bivalents= in black; complex formations= constituted by a bivalent of normal size (in black) and a chromosome element of reduced size (outlined), marked with arrows]; 1.2, 1.2', 1.3 and 1.3'= in diakinesis showing n= 26 II (bivalents of normal size= in black, bivalents of larger dimension= outlined), 1.1, 1.2 and 1.3 from Spain; León, La Vid, town 2 km from Vegacervera, 30TTN85.

SHORT NOTE

ACROSTICHUM AUREUM: AN INLAND RECORD FROM SAUDI ARABIA

There are several remarkable fern and fern-ally occurrences in Saudi Arabia, among them being *Psilotum nudum* (L.) Beauv., *Anogramma leptophylla* (L.) Link, *Cystopteris fragilis* (L.) Bernh., *Pleopeltis macrocarpa* Kaulf. and *Acrostichum aureum* L.

On March 11th 1985 *Acrostichum aureum* was found in Wadi Farshah, a tributary of Wadi Baysh whose headwaters rise on the Yemen border in the southwest of the kingdom of Saudi Arabia. The site, on the north bank of the wadi, is over 100 km inland and lies at an altitude of 2,700 ft. The wadi has some running water most of the year and flows westward through Baysh and into the sea some 50 km north of Jizan; only for the last few km does the stream flow under sand.

At the time of its discovery there were two populations of plants some 25 m apart; the larger was in a slightly saline alkaline seepage of 15 square feet on a sloping rocky bank behind a belt of Dom Palms (*Hyphaene thebaica*) and the ferns grew in the shelter of a thicket of *Phragmites australis* grass and among cushions of the small sedge *Cyperus squarrosus*. The other population, of only a couple of plants, also grows in a seepage, a tiny one, on a ledge on a steep cliff some 12 ft. above the wadi bed (Fig. 1); almost immediately above is a fine specimen of the succulent tree *Adenium obesum*, a strange bedfellow for the 'mangrove fern'.

In Saudi Arabia *Acrostichum aureum* appears to be drought deciduous and in the March of its discovery the new growth of leaves was only a few cm tall, but the dead stems measured nearly 2 m.

The mountainous southwest area of Saudi Arabia is populated by indigenous semi nomadic tribes of Yemeni origin and they used to survive mainly on the produce of herds of ginger coloured goats, bartering cheese and butter for sorghum grown on the fertile plains nearer the sea. Since the oil boom years of the 70's and the introduction of government livestock headage subsidies and cheap grain, many of the tribespeople have bought pick-up trucks and camels, and improved medical facilities have led to a population explosion among the people.

On May 6th 1990 the *Acrostichum* site was revisited; exceptionally heavy rains had washed out the tracks that lie in the wadi bed and in many places the floodwaters came to the level of the floor of the Toyota. Large numbers of camels had eaten most of the bankside shrubs and even the lower leaves of the Dom Palms so that the character of the wadi had changed; if careful note of its 12 km distance from Farshah village had not been recorded in 1985, the site would have been overlooked. The larger population had been reduced to two tiny grazed stumps and the tall grasses, severely overgrazed, were dead. Only the tiny cliff population had survived, being above the reach of camels. The plants had fronds that were only about 1 m long, but they were fertile and living spores were taken by Edinburgh Botanic Garden from the herbarium sheet and an attempt has been made to grow them.

I.S. COLLENETTE
Greenslade, Meadend, Sway, Hants SO41 6EH, England

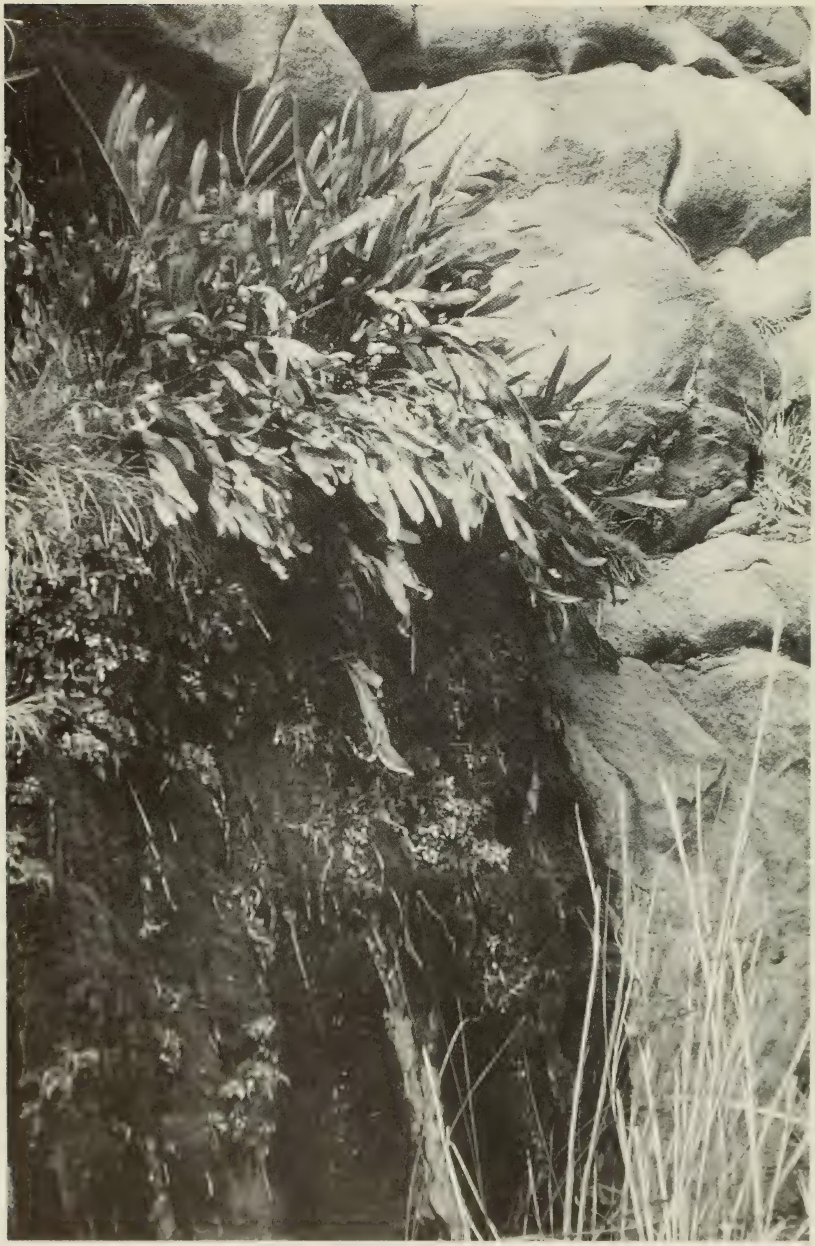

FIGURE 1: Cliff population of *Acrostichum aureum*

THE PALAEOBOTANICAL CASE FOR DIVIDING *SELAGINELLA* (SELAGINELLACEAE: PTERIDOPHYTA)

BARRY A. THOMAS
Botany Department, National Museum of Wales, Cathays Park,
Cardiff CF1 3NP, Wales

NAT QUANSAH
WWF Aires Protégées, B.P. 738, Antananarivo 101, Madagascar.

ABSTRACT

Both isophyllous and anisophyllous forms of *Selaginella*-like plant fossils are known from the late Carboniferous period onwards. This is taken as support for the idea that *Selaginella* should be divided into at least two genera.

INTRODUCTION

Selaginella Beauv. is recognised by most pteridologists as the only genus of extant plants in the family Selaginellaceae Milde. The most recent Code of Botanical Nomenclature (Greuter et al. 1988) lists *Selaginella* Palisot de Beauvoir, Prodr. 101. 1805 as a nomen conservandum in Appendix IIIA. *Selaginoides* Ségguier, Pl. Veron. 3: 51, 1754 is given as its nomenclatural synonym and therefore a nomen rejicendum. *Lycopodiodes* Boehmer in Ludwig, Defin. Gen. Pl. ed.3, 485, 1760 and *Stachygynandrum* Palisot de Beavoir ex Mirbel in Lamark and Mirbel, Hist. Nat. Veg. 3: 477, 1802; 4: 312, 1802 are given as taxonomic synonyms, being based on different types from that of the conserved *Selaginella*. The literature on the subject of the usage of generic names and indeed that of the various proposed subgenera of *Selaginella* is a complex one and more complicated than the Code seems to suggest.

Our observations, over many years, on both living species of *Selaginella* and specimens of very closely related fossil plants suggest that a re-evaluation of the usage of generic and subgeneric names is necessary.

REVIEW OF PERTINENT LITERATURE ON THE TAXONOMY OF LIVING SPECIES

Early classifications (eg. Willdenow 1810; and Sprengel 1827) included *Selaginella* as a synonym of *Lycopodium*, until Spring (1850) presented the major monograph of the genus *Selaginella* outlining it as it is presently understood. However, even though most people have generally understood and agreed on the parameters of the genus *Selaginella*, there have been many attempts to express taxonomically the groupings of recognisably similar species included within it. There have been five major treatments of the genus since Spring's work which divide *Selaginella* into subgenera. These are works by Braun (1865), Baker (1833, 1887), Hieronymus (1901), Walton & Alston (1938) and Jermy (1986). Rothmaler (1944) took a different approach by recognising three distinct genera of Selaginellaceae: *Selaginella* Beauv., *Lycopodioides* Boehmer and *Didiclis* Beauv. These genera, however, have not been accepted by later authors (eg. Bizzari 1975; Tryon & Tryon 1981) who believed that Rothmaler neither examined enough material nor gave enough information about the usage of the genera.

The early monographers (Spring 1850; Braun 1865; Baker 1883, 1887) used plant habit as a criterion for major divisions within the genus. Hieronymus (1901) was an exception for, although using growth characters for establishing two subgenera, he made extensive use of the stelar pattern in his taxonomic treatment. Walton & Alston (1938), Panigrahi & Dixit (1968), Crabbe & Jermy (1976), Alston et al. (1981) and Jermy (1986) have also made use of plant habit as a diagnostic feature.

The taxonomic divisions of the genus by the various authors differed in the number of subgenera, or genera, that were accepted. Spring (1850) and Hieronymus (1901) divided the genus into two subgenera – *Homoeophyllum*, containing taxa with isophyllous leaves, and *Heterophyllum*, containing taxa with anisophyllous leaves. Braun (1865) recognised the same two groups but named them *Homotropae* and *Dichotropae* respectively. In contrast, Baker (1883, 1887) and Walton and Alston (1938) recognized four subgenera – *Selaginella*, (=*Euselaginella*), *Stachygynadrum, Homostachys* and *Heterostachys*. The subgenera *Selaginella* of Baker (1883, 1887) and *Euselaginella* of Walton & Alston (1938) correspond to the *Homoeophyllum* of Spring (1850) and Hieronymus (1901) and the *Homotropae* of Braun (1865), whereas their other three subgenera (*Stachygynandrum, Homostachys* and *Heterostachys*) together correspond to the subgenera *Heterophyllum* of Spring (1850) and Hieronymus (1901) and *Dichotropae* of Braun (1865). Thus, in the systems of Baker (1883, 1887) and Walton & Alston (1938), the subgenus *Selaginella* (=*Euselaginella*) is separated from the other three subgenera on the basis of its isophyllous leaves. The three other subgenera (*Stachygynandrum, Homostachys,* and *Heterostachys*), which are all anisophyllous, are mainly distinguished from each other on the basis of strobilus morphology. Jermy (1986) recognised five sub-genera; three of which, *Selaginella, Ericetorum* and *Tetragonostachys*, are isophyllous and two, *Stachygynandrum* and *Heterostachys*, are anisophyllous.

From the results of a study of West African and Madagascan species of *Selaginella* (Quansah 1986) and a preliminary review of some 100 South American species (Quansah & Thomas 1985), we see justification for dividing the genus into at least two major groups. We recognize one group containing species with isophyllous leaves and another containing species with anisophyllous leaves. In this we clearly agree with several recent workers, including Jermy et al. (1967), Crabbe & Jermy (1976), Alston et al. (1981), and Tryon & Tryon (1981), who have recognized two subgenera, *Selaginella* and *Stachygynandrum*, within the genus. The two groups are in fact retained from Baker's (1883, 1887) usages of two subgenera within his classification. The other two subgenera, *Homostachys* and *Heterostachys*, recognized by Baker and by Walton & Alston (1938) are thought to be better included within a single taxonomic unit containing all the anisophyllous species.

EVIDENCE FROM THE FOSSIL RECORD

Herbaceous lycophytes have a fossil record of over 400 million years, being known from the Upper Silurian to the present day. The earliest, *Baragwanathia* Lang & Cookson (1935) came from Upper Silurian strata of Victoria, Australia (Garratt et al. 1984), while *Drepanophycus* Goeppert (1852) and *Asteroxylon* Kidston & Lang (1920) came from the Lower Devonian of the Northern Hemisphere. These must have been very much like living *Huperzia selago* (L.) Bernh. ex Schrank & Mart. in size, general morphology, in being homosporous and, as far as we know, in stelar anatomy. The earliest homosporous forms diversified and evolved in many ways, for hybridization was probably easily accomplished through their simple genetic makeup. Some forms seem to have continued almost unchanged to the present day, others evolved into further homosporous and heterosporous herbaceous forms, while some evolved along quite different paths that gave rise to the arborescent Carboniferous lycophytes and the extant Isoetales.

Heterospory is presumed to have developed in several groups of plants during the late Devonian, as the record of fossil spores shows a rapid increase in the number and diversity of larger spores (presumed megaspores) during this period (Chaloner 1967). Heterosporous lycophytes are known from the Lower Carboniferous onwards.

In the Carboniferous floras of the equatorial Euramerian area (now Europe, eastern Northern America and northern Africa) herbaceous forms appeared that had very similar morphologies to extant species of *Selaginella*. These fairly rare species have usually been placed into the genus *Selaginellites* Zeiller (1906), which was first used for a specimen from the Blanzy Coalfield (Upper Carboniferous) in France that he named *Selaginellites suissei*. This lycophyte had a dichotomously branched stem, dimorphic leaves, and a terminal bisporangiate cone with apical microsporangia and basal megasporangia. *Selaginellites suissei* is therefore very similar to many living anisophyllous species of *Selaginella* that have tetragonous strobili eg. *Selaginell vogelii* Spring, *S cathedrifolia* Spring and *S. pervillei* Spring (Quansah 1988).

There are several other species of anisophyllous *Selaginellites* that have been described from the Upper Carboniferous Coal Measures. The rather fine specimen of *Selaginellites gutbieri* (Goeppert) Kidston (1911) as figured by Schimper (1870-72, pl.57, fig.4) and Hirmer (1927, fig.327) has been re-examined by one of us (B.A.T.) and confirmed to be anisophyllous with terminal cones. Microspores have been recovered from several of the cones, although no megaspores were found. It is, however, quite possible that the plant had only microsporangia similar to the condition found in some plants of many living anisophyllous species of *Selaginella* e.g. *S. versicolor* Spring, *S. vogelii* Spring and *S. leonensis* Hieron. (Quansah 1988). *Selaginellites elongata* Goldenberg is however rather different. It was re-examined by Halle (1907) who described the sporangia as occurring in the axils of ordinary vegetative leaves. This, however, seems to us to be quite possibly the condition found in such living species as *Selaginella denticulata* (L.) Link and *S. pallidissima* Spring where there are two sizes of sporophylls arranged in four ranks. In these living species the smaller sporophylls are in the same plane as the smaller median vegetative leaves and the larger sporophylls are in the same plane as the larger lateral vegetative leaves (Quansah 1986). This gives the superficial appearance of there not being a discrete cone.

Anisophyllous forms of *Selaginellites* have also been described from Mesozoic strata and many of these have been shown to be heterosporous (eg. Ash 1972; Harris 1935, 1961; Lundblad 1950; Watson 1969).

Some anisophyllous forms of plant fossils have, however, been included in the genus *Lycopodites* as used by Brongniart (1822) or by Lindley & Hutton (1833). This name has been given to small leafy shoots of presumed herbaceous lycophytes, that are either homosporous or of unknown spore content, from the Carboniferous onwards. Unfortunately, it is not a satisfactory taxonomic unit having been used for both isophyllous and anisophyllous species. Some specimens included in *Lycopodites* have even been subsequently shown to be twigs of larger lycophytes or conifers, or even an hepatic (*Naiadita*). Pal & Ghosha (1990) have discussed the confusion resulting from Brongniart's use of *Lycopodites* for a type species whose affinities are not at all clear. They recommended the conservation of *Lycopodites* Lindley & Hutton against *Lycopodites* Brongniart.

The type species *Lycopodites falcatus* Lindley & Hutton emend. Harris (1961) has two ranks of larger lateral leaves and two ranks of smaller leaves, but the latter are only half as numerous as the former. This is unlike the arrangement in extant *Selaginella* where there are equal numbers of the two sorts and was taken by Harris (1961) as being more like the arrangement in *Lycopodium volubile* Forst, or *Lycopodium complanatum* L.

Isophyllous forms referrable to *Selaginellites* are known from the Lower Carboniferous onwards. Rowe (1988) has described the earliest (*S. resimus*) from the Drybrook Sandstone of the Forest of Dean, Gloucestershire. Others, such as *S. fraiponti* (Leclerq) Schlanker & Leisman (1969), are known from the Upper Carboniferous Euramerian Coal Measures, although they are very rare. This species has been described as sparsely branched, sprawling and possibly of determinate growth. The terminal cone had its sporophylls arranged in alternating pairs of verticils. It is, therefore, very similar in morphology to some species of living *Selaginella*, eg. *S. selaginoides* L., except for not having a distinctive basal root-bearing organ.

Both anisophyllous and isophyllous forms of *Selaginella*-like plants are, therefore, known from the Upper Carboniferous onwards and some of these have even been thought to be generically indistinguishable from *Selaginella* itself.

THE GENERIC ASSIGNMENT OF FOSSIL PLANTS

There has been a great deal of debate about the necessity of having another genus for fossil plants in preference to *Selaginella* as used for extant species. Zeiller (1906) originally suggested that the presence of more than four megaspores in each megasporangium was a distinguishing feature for his new genus *Selaginellites*. Halle (1907) did not accept that this character was necessary and used *Selaginellites* for all heterosporous fossils. Since then it has been shown that living species of *Selaginella* can possess more than four megaspores per sporangium (Duerden 1929, Quansah 1988). Seward (1910), Harris (1935) and Chaloner (1967) have all used *Selaginellites* for all fossil shoots that were closer to *Selaginella* than any other genus. In contrast, Darrah (1938), Lundblad (1950), Townrow (1968), Schlanker & Leisman (1969), Watson (1969) and Ash (1972) have used *Selaginella* for fossil shoots because they could not show any real morphological differences between them and the extant species of that genus.

Plant fossils are often incomplete fragments of the original whole organism, a condition which poses even more problems for taxonomy and nomenclature (See Collinson 1986 and Thomas 1990 for general discussions). Lundblad (1948) assigned a small detached heterosporous cone to a new species, *Selaginellites polaris*, even though its relative stoutness meant that it does not compare very well with the general aspect of *Selaginella* cones. When the fossils are merely vegetative shoots a decision has to be made without evidence of their reproductive organs. Some authors have suggested referring all vegetative shoots to *Lycopodites* believing that it is impossible to assign them to *Selaginellites* (or *Selaginella*) without evidence of heterospory. Anisophylly was thought to be of insufficient evidence. However, as shown above, Harris (1961) demonstrated that the type specimen of *Lycopodites* Lindley & Hutton had unequal numbers of larger and smaller leaves.

Taking all the available evidence into account, we believe that both fertile and vegetative anisophyllous *Selaginella*-like plant fossils, with equal numbers of larger and smaller leaves, can be referred to the same genus. It does not, however, seem logical to include the isophyllous *Selaginella*-like plant fossils in this genus. Even if the isophyllous and anisophyllous forms originated from a common ancestral group, they have been recognisable as two discrete morphological forms for nearly 300 million years. This we regard as valuable evidence for regarding the two groups of plants as taxonomically distinct.

CONCLUSION

Evidence from both the living species and the fossil plants, showing that there have been two clearly different morphological forms from the Upper Carboniferous onwards, provides a clear case for formalising the taxonomical distinction of at least two genera. We believe that the recognisable division of the genus into isophyllous and anisophyllous forms over 300 million years ago provides an overwhelming reason for making this distinction at the generic rather than the sub-generic level.

There is a strong case, based on living plants, to divide *Selaginella* into more than two genera. At the moment, however, there is not sufficient palaeobotanical evidence to support this case. The reason for this may be because fossil plants are so often only preserved as fragments, so future discoveries might provide further evidence. Nevertheless it is a statement of our present knowledge. Therefore, if several genera of anisophyllous species were created, it would be virtually impossible to assign a fossil to any one of them. This would force palaeobotanists back into using one or more different names specific to fossils.

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THE SYSTEMATIC STATUS OF *MATTEUCCIA INTERMEDIA* (WOODSIACEAE: PTERIDOPHYTA)

M. KATO & T. SUZUKI
Botanical Gardens, Faculty of Science, University of Tokyo,
3-7-1 Hakusan, Tokyo 112

N. NAKATO
Shinjuku High School, Sendagaya, Tokyo 151, Japan

ABSTRACT

Matteuccia intermedia is morphologically so roughly intermediate between *M. struthiopteris* and *Onoclea orientalis* that it has been suggested to be of hybrid origin between the latter two species. *Matteuccia intermedia* has prominent pneumatophores at the base of the stipe, an almost flat adaxial side of the stipe and rhachis, and the chromosome number 2n=80, and did not show a combination of enzyme bands either of which is the same as that of either of the formally presumed parental species for the 14 allozymes examined, among which were seven unique enzyme bands. These three features indicate that *M. intermedia* is not a hybrid nor a species of recent hybrid origin but a distinct species, obviously related to *O. orientalis*. A nomenclatural combination to *Onoclea* is proposed – ***O. intermedia*** (C.Chr.) Kato, T. Suzuki & Nakato **comb.nov.**

INTRODUCTION

Matteuccia intermedia C. Chr. is an enigmatic onocleoid species, distributed in eastern Asia from the eastern Himalayas to China (Heibei, Shansi, Shensi, Hubei, Kansu, Sichuan, Yunnan, east Tibet). Morphologically it is roughly intermediate between *M. struthiopteris* (L.) Todaro and *Onoclea orientalis* (Hooker) Hooker [=*Matteuccia orientalis* (Hooker) Trev.], resembles *M. struthiopteris* in its erect or ascending rhizome and oblong lamina with a narrowed base, and resembles *O. orientalis* in its scaly, long stipes and cylindrical fertile pinnae (Christensen 1913, Lloyd 1971, Kato & Sahashi 1980). However, *M. intermedia* differs from these two species in its shallowly lobed sterile pinnae and exindusiate sori (Christensen 1913). Christensen (1913) considered *M. intermedia* to be perhaps nearest to *O. orientalis*. When establishing the genus *Pentarhizidium* segregated from *Matteuccia*, based on *P. japonica* Hayata (=*O. orientalis*), Hayata (1928) placed *M. intermedia* in *Pentarhizidium*. Lloyd (1971) suggested that *M. intermedia* is an allopolyploid derivative of a cross between diploid *M. struthiopteris* and diploid *O. orientalis* because of its morphological intermediacy, although no cytological data were available. Tryon & Tyron (1982) stated that *M. intermedia* may be a distinct species or a small form of *O. orientalis*.

Most authors (e.g. Lloyd 1971) classified the onocleoid ferns in three genera: *Matteuccia* of three species, a monotypic *Onoclea*, and a monotypic *Onocleopsis*. In this classification *M. intermedia* belongs to *Matteuccia*. By contrast, Kato & Sahashi (1980) divided the group into two genera: *Matteuccia,* consisting of *M. struthiopteris* and *M. hintonii* (F. Ballard) Kato (type species of the genus *Onocleopsis*), and *Onoclea* of *O. orientalis* and *O. sensibilis* L. Kato & Sahashi did not place *M. intermedia* in either of the two revised genera, and tentatively treated it as an intergeneric hybrid.

In order to determine the systematic position of *M. intermedia*, chromosomal and genotypic evidence were needed. The present study attempts to resolve the systematic puzzle of *M. intermedia* by means of comparative morphology and cytotaxonomic and electrophoretic analyses.

MATERIALS AND METHODS

Materials used in this study are listed in Table 1. Voucher specimens are deposited in the Herbarium, Botanical Gardens, Faculty of Science, University of Tokyo (TI). For chromosome observations of *M. intermedia* and *O. orientalis* (Kato et al. 2130), root tips were pretreated with 0.05% colchicine for 3-4 hours at about 20° C, fixed in Newcomer's fluid (Nishiyama 1961) and transferred to another volume of Newcomer's solution one week after fixation. They were hydrated in a series of 99%, 70%, 50%, and 30% ethanol, and distilled water each for 2-3 minutes. At the 30%-ethanol and water washing stages, the root tips were cleaned with ultrawave. They were macerated in a mixture of 4% cellulase and 2% pectolyase (pH 4) at 37° C for one hour. The macerated root tips were washed with distilled water, then stained and squashed in 2% aceto-orcein. For chromosome observations of *M. struthiopteris* and *O. orientalis* (Kato H336, Nakato 1655), root tips were pretreated with 0.002 M 8-hydroxyquinoline solution in darkness at about 20° C for 3 hours, fixed in 45% acetic acid for 10 minutes, macerated in a mixture of 1 N HC1 and 45% acetic acid (2:1) at 60° C for 2-3 minutes, and then stained and squashed in 2% aceto-orcein.

Enzyme electrophoresis was employed for genotypic comparison between *M. intermedia*, *M. struthiopteris*, and *O. orientalis*. Enzymes analyzed were aconitase (ACN), aldolase (ALD), fructose-1,6-diphosphatase (F1,6DP), esterase (fluorescent) (FE), glutamate dehydrogenase (GDH), hexokinase (HK), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), 6-phosphogluconate dehydrogenase (6-PGD), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase (SkDH), and triosephosphate isomerase (TPI). Portions of young leaves were ground with an extracting buffer of 0.1 M Tris-HC1, pH 7.5, 1 mM EDTA (tetrasodium salt), 10 mM KC1, 10 mM $MgC1_2$, 0.2% (v/v) 2-mercaptoethanol, 0.5% sodium L-ascorbate, 0.5% sodium metabisulfite, and 5% PVP (Sigma 40T). The crude extracts were centrifuged and the supernatants were used for elecrophoresis. With 11.8% starch gels, ALD, GDH, LAP and TPI were resolved on electrode buffer system 8 of Soltis et al. (1983), and ACN, F1,6DP, IDH, 6-PGD, PGM and SkDH on a system of histidine-citrate, pH 6.5 (Cardy et al. 1981). With acrylamide gels (T=5%, C=5%) FE, HK and PGI were resolved on a modification of the buffer system 8. Staining schedules followed those of Soltis et al. (1983).

RESULTS

Stipe and rhachis

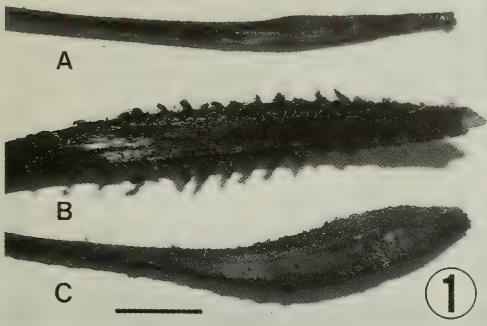
The stipe-base of *Matteuccia intermedia* is swollen as in *M. struthiopteris* and *O. orientalis*, and is long and gradually narrowed to its insertion on the rhizome as in *M. struthiopteris* (Fig. 1). A row of prominent pneumatophores is present on each side of the stipe-base in *M. intermedia*. Such pneumatophores are very short in *O. orientalis* and lacking in *M. struthiopteris*. The adaxial side of the stipe and rhachis of *M. intermedia* is almost flat, or only shallowly grooved as in *O. orientalis*, and not deeply grooved as in *M. struthiopteris* (Fig. 2).

Chromosomes

Matteuccia intermedia had 2n=80 in two plants (Kato et al. 2131, Fig. 3A; 2132), and *M. struthiopteris* had 2n=78 in a Japanese specimen (Nakato 1680, Fig. 3B). *Onoclea orientalis* showed 2n=80 or ca. 80 in one Japanese and two Chinese plants (Nakato 1655; Kato H336, Fig. 3C; Kato et al. 2130). The three species are, therefore, all regarded as diploid. The chromosomal data are summarized in Table 1.

Enzyme electrophoresis

The results of the electrophoretic analysis are shown in Table 2. Of the 14 allozymes examined, *M. intermedia* had enzyme bands (and interpreted alleles) of ACN, F1,6DP, FE, HK, LAP, 6-PGD, and PGI-2, which differed from those of both *M. struthiopteris* and *O. orientalis*. *Matteuccia intermedia* had the same band of PGM-2 as that of *M. struthiopteris*, and the same bands of ALD, IDH, TPI-1, and TPI-2 as those of *O. orientalis*. All three species had the same bands of GDH and SkDH.



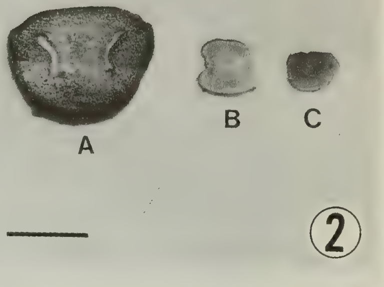


FIGURE 1. Stipe-bases of *Matteuccia struthiopteris* (A), *M. intermedia* (B) and *Onoclea orientalis* (C). Scale bar=2 cm.

FIGURE 2. Cross sections of leaf-axes of *Matteuccia intermedia*. A. Stipe-base of sterile leaf. B. Middle portion of rhachis of sterile leaf. C. Middle portion of rhachis of fertile leaf. Scale bar=5 mm.

DISCUSSION

Our chromosomal evidence does not indicate that *Matteuccia intermedia* is an allotetraploid derivative of a hybrid between *M. struthiopteris* and *O. orientalis*, as suggested by Lloyd (1971), nor that it is a diploid hybrid between the two species. The present study confirms that the basic chromosome number of *M. struthiopteris* (x=39) differs from that of *O. orientalis* (x=40). Although the chromosome number of *M. struthiopteris* has been reported to be x=40 (Lloyd 1971, Löve et al. 1977), the present and other recent studies show that it is x=39 for Asian, North American and European plants (Fabbri & Menicante 1970, Löve 1976, Kurita 1976, Wang & Zhang 1981). *Matteuccia intermedia* and *O. orientalis* are diploids with the same base number x=40, which suggests a closer affinity of *M. intermedia* to *O. orientalis* than to *M. struthiopteris*.

The present electrophoretic evidence also suggests that *M. intermedia* is not a hybrid nor perhaps a species of recent hybrid origin from *M. struthiopteris* and *O. orientalis*, even though all the materials were not collected from the same or neighbouring localities in Yunnan. A hybrid or a species of recent hybrid origin would be expected to have enzyme bands (and alleles coding allozymes) derived from those of both parental species. For any allozyme examined, *M. intermedia* did not show a combination of enzyme bands like those of either *M. struthiopteris* or *O. orientalis*, but for seven allozymes it showed unique bands.

Matteuccia intermedia differs morphologically from *M. struthiopteris* and *O. orientalis* in its shallowly lobed sterile pinnae, exindusiate sori (Christensen 1913, Lloyd 1971) and prominent pneumatophores at stipe-bases (present study). *Matteuccia intermedia* is, therefore, here considered to be a species amply distinct from *M. struthiopteris* and *O. orientalis*.

Kato & Sahashi (1980) used a leaf-axial character to revise the two genera *Onoclea* and *Matteuccia*. The adaxial side of the stipe and rhachis is almost flat or only shallowly grooved in *Onoclea*, but is deeply grooved in *Matteuccia*. In this character *M. intermedia* is similar to *O. orientalis* and *O. sensibilis*. Thus morphological and above-noted chromosomal similarities indicate that *M. intermedia* is more closely related to *O. orientalis* rather than to *M. struthiopteris*.

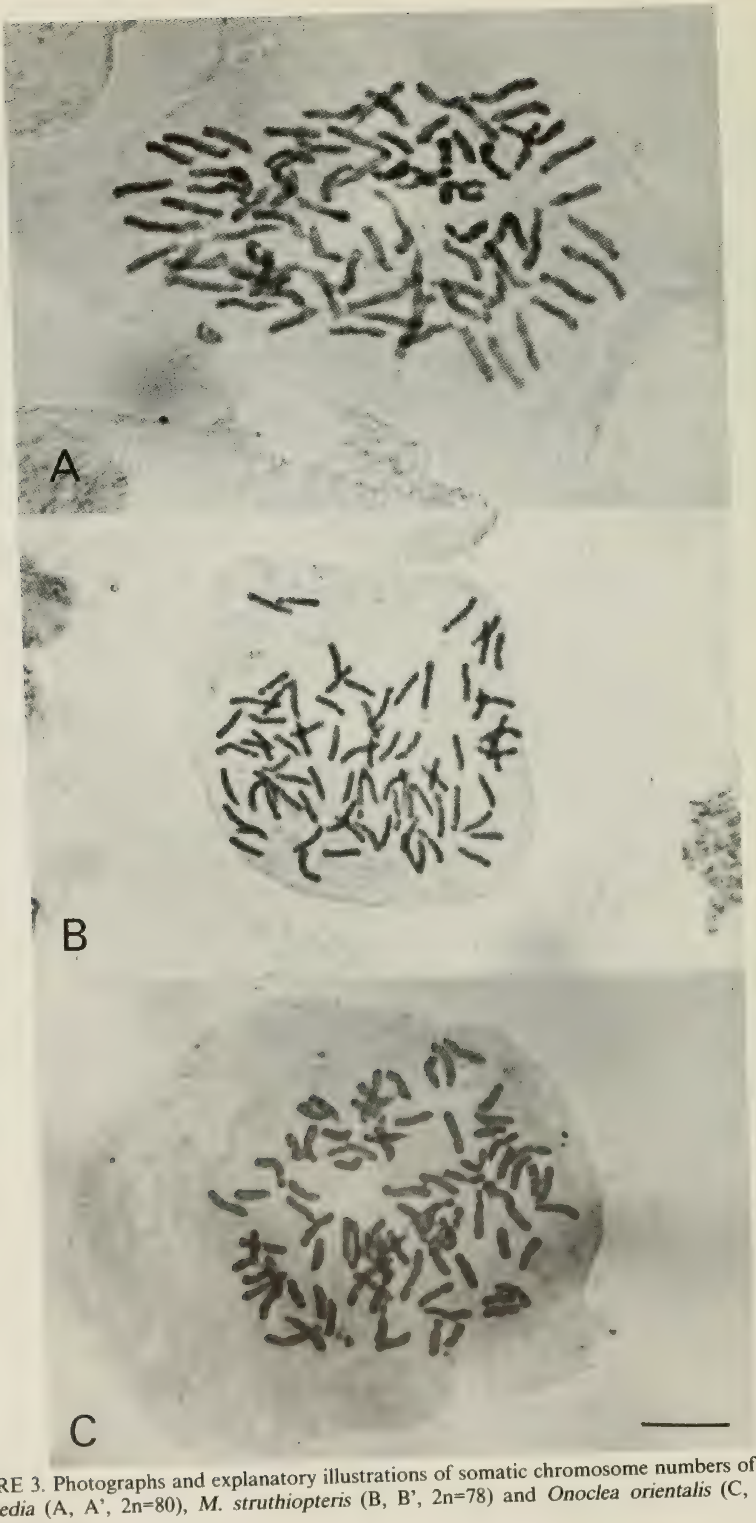
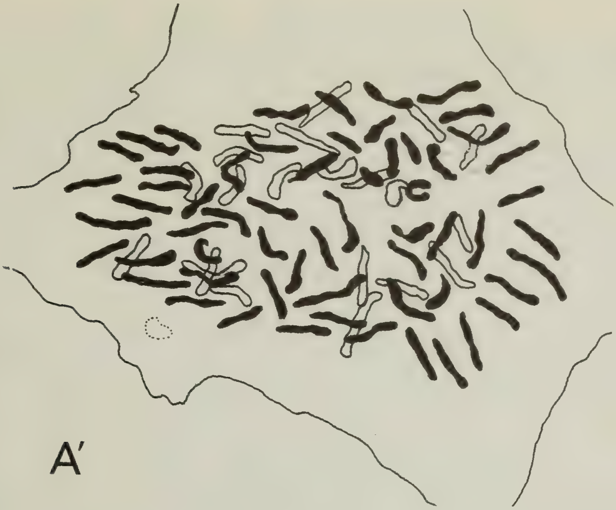
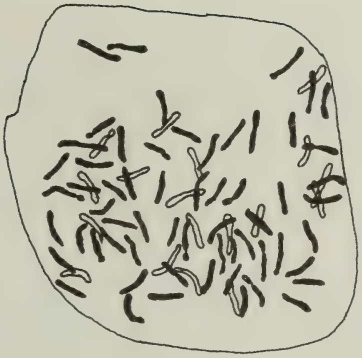


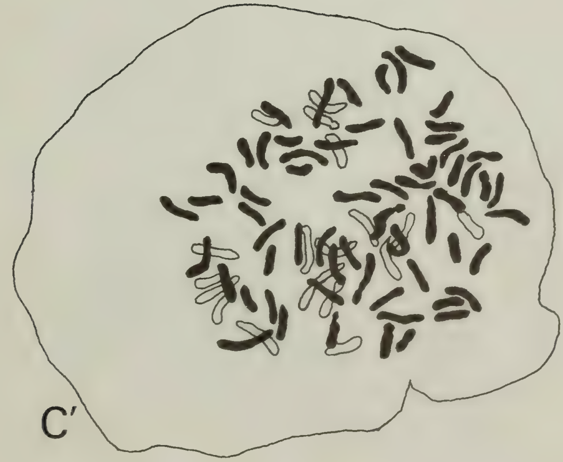
FIGURE 3. Photographs and explanatory illustrations of somatic chromosome numbers of *Matteuccia intermedia* (A, A', 2n=80), *M. struthiopteris* (B, B', 2n=78) and *Onoclea orientalis* (C, C', 2n=80). Scale bar=10 µm.



A′



B′



C′

TABLE 1.
Materials used in this study and chromosome numbers counted

Species	Locality & voucher	Chromosome number (2n)
Matteuccia intermedia	Zhonghe temple, Yunnan; Kato et al. 75(1)*	–
	Swangian stream, Yunnan; Kato et al. 2131	80
	Swangian stream, Yunnan; Kato et al. 2132	80
M. struthiopteris	Botanical Gardens, University of Tokyo; no voucher (3)*	–
	Higashiyamato (cult.); Nakato 1680	78
Onoclea orientalis	Swangian stream, Yunnan; Kato H336 (1)*	80
	Swangian stream, Yunnan; Kato et al. 2130	c.80
	Tanzawa, Kanagawa Pref.; Nakato 1655	80

* Materials used for enzyme electrophoresis. Individual numbers are shown in parentheses.

TABLE 2.
Allozyme comparison of *Matteuccia intermedia, M. struthiopteris* and *Onoclea orientalis*. Different letters in each allozyme indicate different bands

Allozyme	*M. struthiopteris*	*M. intermedia*	*O. orientalis*
ACN	a	c	b
ALD	b	a	a
F1, 6DP	a	c	b
FE	a	b	c
GDH	a	a	a
HK	a	b	a
IDH	b	a	a
LAP	c	a	b
6-PGD	e	c, d	a, b
PGI-2	a	b	a
PGM-2	b	b	a
SkDH	a	a	a
TPI-1	b	a	a
TPI-2	b	a	a

Matteuccia intermedia is formally transferred to the genus *Onoclea*, as follows:

> ***Onoclea intermedia*** (C. Chr.) Kato, T. Suzuki & Nakato, **comb. nov.** – *Matteuccia intermedia* C. Chr., *Bot. Gaz. 56:* 337, 1913; Lloyd, *Univ. Calif. Publ. Bot. 61:* 71, pl. 5a-c, 1971. – *Pentarhizidium intermedium* (C. Chr.) Hayata, *Bot. Mag. Tokyo 42:* 346, 1928. – *Pteretis intermedia* (C. Chr.) Ching, *Lingnan Sci. J. 21:* 36, 1945. According to Christensen (1913), *Struthiopteris orientalis* var. *brevipes* Christ, *Bull. Soc. Bot. France 1:* 44, 1905, is possibly *O. intermedia.*

Accepting Kato's bigeneric classification system of the onocleoid ferns (Kato & Sahashi 1980), the most ancestrally representative species are *Onoclea sensibilis* and *Matteuccia hintonii* both with reticulate venation, while *O. orientalis* and *M. struthiopteris* with free venation are more derivative. It is assumed that the evolutionary trend of the onocleoid ferns is towards simplification in venation, sporophyll dissection (tri- or bipinnate to simply pinnate), and sori (discrete to coenosoral) (Kato & Sahashi 1980). It follows that *O. intermedia* is an advanced species in the genus *Onoclea*, and the lack of indusia is a further derivative character state in the onocleoid ferns.

ACKNOWLEDGMENTS

We are grateful to Prof. K. Iwatsuki, Drs N. Murakami, S. Akiyama, Y. Shimizu, X. Chen, and S.-J Lin for their help in the field survey and to the Director, Kunming Institute of Botany, the Academy of Sciences of China, for the collaborative research. Our thanks are particularly due to Dr M. Wakabayashi for his cytological-technical assistance and to Dr M. G. Price for his critical reading of the manuscript. We are also indebted to Mr K. Hirai who cared for the living plants of onocleoid ferns in the Botanical Gardens, Faculty of Science, University of Tokyo. This study was partly supported by Grants-in-Aid, 63041049 and 02041026 to K. Iwatsuki, for Monbusho International Scientific Research Program, and 02454017 to K.I., for Scientific Research from the Ministry of Education, Science and Culture, Japan.

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REVIEW

continued from page 54

The 50 papers that follow are grouped into General, Biosystematics, Geography, Ecology and floristics. Morphology and anatomy, Chemistry and medicine, and Palaeobotany. It would be invidious to select any individual papers for comment; authors from 11 countries have contributed and it is good to see the work of over 40 Chinese pteridologists getting into print. A volume reprinting 12 of the more substantial papers, with a full bibliography of all of Ching's work was published by the Academia Sinica, Beijing (ISBN 7-03-00753-O/Q 121) in 1988 to link with the Symposium.

A.C. JERMY

CORRIGENDA

On the front cover of *Gazette* 14(1) it should have said it was Edited by J.A. Crabbe; on the inside the following should be corrected:

The date given for the Officers and Committee should have been 1991.

Three subscription rates and one postage rate had increased.

The Society's journals, the *Pteridologist* and the *Bulletin* are published annually; the *Fern Gazette* is now published twice a year.

The Fern Distribution Recorder has moved to Norfolk.

THE SPORES AND AFFINITIES OF *ISOETES TAIWANENSIS* (ISOETACEAE: PTERIDOPHYTA)

DONALD M. BRITTON
Department of Molecular Biology and Genetics, University of Guelph, Guelph,
Ontario N1G 2W1

DANIEL F. BRUNTON
216 Lincoln Heights Road, Ottaway, Ontario K2B 8A8, Canada

ABSTRACT

Errors in the original illustration of megaspores of *Isoetes taiwanensis* De Vol invite confusion in regards to the identification and affinity of this rare Taiwan endemic. As a basic sexual diploid it is important to an understanding of the taxonomy and evolution of *Isoetes* in the western Pacific – Australasian area. A re-examination of a majority of the extant material for this species offers a series of SEM photographs of typical microspores and megaspores and explores its affinity with other *Isoetes* species. We conclude that *I. taiwanensis* is probably a member of a complex of high elevation, cold water, island species occurring along the western Pacific rim from New Zealand to Taiwan, with derivative polyploids in the Philippines and New Guinea. We do not believe it to be closely related to southwestern Australian taxa as has been previusly suggested. It appears to have closest affinity to *I. kirkii* A. Br., a diploid New Zealand endemic. There is also evidence that hybrids, although not previously reported from the southern hemisphere, are of regular occurrence amongst the Australian species. The Australian *Isoetes drummondii* A. Br. var. *anomala* Marsden is particularly likely to prove to be of hybrid origin.

INTRODUCTION

Marsden (1979) in a Ph.D. thesis entitled "Morphology and Taxonomy of *Isoetes* in Australasia, India, North-East and South-East Asia, China and Japan", concluded that there were 29 species in this segment of the globe. Of these 29 species, 14 (plus one subspecies of an Indian species – Marsden 1976a) were from Australia, six from India, four from New Guinea (Croft 1980), two from Japan and one from each of the Philippines (Merrill and Perry 1940), New Zealand, Taiwain and China. A major contribution of Marsden's (1979) study was a large series of Scanning Electron Microscope (SEM) photographs (Figures 13-294) of megaspores (27 species) and microspores (20 species). Marsden did not have material with megaspores of *Isoetes taiwanensis* De Vol, however, and this contributed to some lost opportunities in his study.

Accordingly, having had the opportunity of examining the majority of known *I. taiwanensis* material, we are undertaking in this paper to describe the spores of *I. taiwanensis,* to indicate why it is an important species in the evolution of *Isoetes* and to speculate on its affinities with other species in Marsden's (1979) study area. It is a rare species, known only from a small, shallow pond at ca. 1000 m elevation near the top of an extinct volcano (De Vol 1972a). It is abundant here (the dominant plant) and persists as a true aquatic or occasionally as an emergent along the pond's peaty shores.

MATERIALS AND METHODS

We received six sheets in a loan from TAI. Four collections were mounted on herbarium paper and two were loose plants in newspapers. Since material of *I. taiwanensis* is rare and Marsden (1979) was unable to find megaspores from two sheets at BM and was reduced to picking a few loose microspores off a sheet (a dangerous expedient), the sheets from TAI are detailed here:

1. *K. S. Hsu 1715,* 22 August 1971, Chih-Sing-Shan, Taipei County, Taiwan. Shallow pond, abundant, 800 m. (TAI 140877) HOLOTYPE.
2. *K. S. Hsu 1715,* data as Holotype (TAI 140876) ISOTYTPE.

3. *T. C. Huang 5896,* 1 June 1972, location and habitat as Holotype (TAI 162026) – no sporangia – *not* an *Isoetes.*
4. *T. C. Huang 6186,* 13 September 1972, location and habitat as Holotype (TAI, no number).
5. (unmounted sheet) *T. C. Huang and K. C. Yang 13557-7,* 6 July 1988, Chihsingshan [Chih-Sing-Shan] Taipei (TAI, no number), Det. T. C. Huang.
6. (unmounted sheet) *T. C. Huang and K. C. Yang 13558-2,* 6 July 1988, as sheet 5, above, (TAI, no number).

De Vol (1972a) cites the Holotype as *K. S. Hsu and H. J. Chang 1715,* collected Aug. 22, 1971 from Taipei County, Chong Hu, Seven Star Mt. (specimen in TAI). He notes three other extant collections: *M. T. Kao 7935, De Vol 8005* and *C. C. Hsu 11261,* all from the type location. The two plants studied by Marsden (1979) from BM were from the *K. S. Hsu 11261* Topotype collected 28 December 1971.

We obtained a series of SEM photographs of microspores and megaspores from all five *I. taiwanensis* sheets studied, employing the standard SEM methods described in Britton and Brunton (1989). Spore measurements were made following the protocol given in Britton (1991). To conserve megaspores of the Holotype, measurements were made from sheet 5. A sporewell was made (Brunton 1990) from each sample examined.

A review of world *Isoetes* literature indicates both a striking absence of clear cut characters was well as the variabilities of characters used in classification. Leaf characters (length, width, reflection, stomates, etc.) are notoriously variable (Kott and Britton 1985; Hickey 1986). Marsden (1979) concludes that the best characters for comparison purposes in his study area are (in order of priority): 1. presence or absence of a velum over the sporangium, 2. size and morphology of spores under SEM, and 3. leaf anatomical characters. With the benefit of subsequent research to draw upon, our reconsideration of his data includes several other characteristics, with an emphasis first and foremost on ploidy. Our approach is to, 1. identify the basic diploids, then determine the derived polyploids and the degree of hybridity in the group, 2. consider the phytogeography of the taxa, 3.undertake a SEM assessment of spore morphology and size, 4. consider the ecology of the species and species groups, 5. determine the presence or absence of a sporangial velum, and 6. consider specialized leaf anatomical characters (e.g. internal hairs, peripheral fibre strands, etc. – cf. Hall 1971).

RESULTS

SEM photography

Twenty-one photographs were obtained, representing all five *Isoetes* sheets. Nine have been selected for illustration here. Figures 1a and 1b are distal views of the megaspores, Figures 1c and 1d are lateral views and Figures 1e and 1f are proximal or triradial views. Material from the Holotype is shown on the left side (Figures 1a, 1c, 1e). Figures 1a and 1c represent the full expression of ornamentation of the megaspores in *I. taiwanensis.* Figure 1e shows a spore that is rather eroded or weatherworn but is noteworthy for the broad, triradial ridges which are so striking in Figure 1f. Figures 1b and 1f are perhaps less mature megaspores, or at least show a decreased expression of ornamentation (more levigate). De Vol (1972b) illustrates two photographs (Figures 3 and 4) of megaspores taken under a light microscope. The impression from his Figure 3 is similar to our Figure 1d. The distal face portion of his Figure 4 is similar to our Figure 1a while the proximal face portion of his Figure 4 is similar to our Figure 1f. The SEM photographs, of course, provide more detail of the suppressed recticulation and the formation of rounded tubercles than is possible with a light microscope.

De Vol (1972a) has a SEM photograph of the distal view of a megaspore (Plate 1, Figure c). This figure is withdrawn in Devol (1972b); it is actually a photograph of a megaspore of the Indian species, *I. pantii* Goswami & Arya. He substitutes light microscope photographs as Figures 3 and 4 (De Vol 1972b) for the erroneous SEM photograph.

Figure 2a shows a full expression of the conical spines on microspores from sheet 6, whereas Figure 2b from the Isotype (sheet 2) illustrates very long, less regularly arranged spines. Figure 2c from sheet 5 shows shorter, bent spines and with some holes from decapitated spines. The degree of spininess in Figure 2 is more pronounced than that shown in Marsden (1979) in his Figures 253 and 254. We consider the microspores shown by him to be either immature or possibly from another species, as they were loose on the herbarium sheet.

Spore measurements

The length of twenty microspores was measured from each of three sheets. The mean for the Holotype (sheet 1), sheet 5 and sheet 6 were 25.6 µm, 23.1 µm and 21.7 µm, respectively. The grand mean was 23.5 um.

Megaspore diameter was calculated from samples from sheet 5 (n=15) to be x = 356 um (325-425 µm). This compares with x = 350 µm (310-390 µm) as given by De Vol (1972a).

DISCUSSION

Spore size and cytology

SEM shows that *Isoetes taiwanensis* has distinctive spores which are small (megaspores x = 365 µm and microspores x = 2.35 µm). The species, as one would expect from such small spores, is diploid 2n = 22 (De Vol 1972a). As a sexual diploid it may be considered as a possible ancestor for derived polyploids, apomicts and possible hybrids.

Marsden's (1979) study is the largest source of data on the *Isoetes* of Australasia, India and the western Pacific. A close examination of these data, therefore, is necessary to developing a taxonomic and evolutionary understanding of *I. taiwanensis.* We take strong exception, however, to Marsden's (1979) statements (pages 53 and 167) that " . . . chromosome numbers alone are of little taxonomic value as almost all species show a base number of n = 11, although numerous polyploids have been recorded and this consistency of chromosome number limits the usefulness of such data in the investigation of phylogenetic relationships between species ... Cytological information ... is also of little assistance in the study of the evolution of the genus". It seems that the correlation between ploidy and spore size was not appreciated by Marsden (1976a, 1976b, 1979).

The easiest approach to investigating the relationship between ploidy and spore size is through determination of the mean microspore length of cytologically determined material (Kott and Britton 1983; Britton 1991). Unfortunately we are not told how Marsden (1979) developed these data (viz, the medium the microspores were in, the number of spores measured, the methodology followed etc.). The need for a reliable standard method (cf. Britton 1991) to provide confidence for interpreting the important "Plot of Size Ranges of Microspore Lengths" (Figure 245) of Marsden (1979) is critical. It would be desirable for analysis to be able to correlate data from this chart with chromosome numbers.

Another interpretation difficulty with Marsden (1979) is that chromosome numbers for only 12 of the 29 species had been obtained at that time. The broad range of microspore lengths for some species (e.g. *I. drummondii* A. Br.) creates further interpretation and correlation problems.

There are some strange anomalies when one compares Marsden's (1979) data in Figure 345 (microspore length) with Figure 344 (megaspore sizes) that can only be clarified with further work. For example, one can derive the mean microspore length for *I. gunnii* A.Br. from the bar in Figure 345 as x= 31-32 um, which is small. This suggests diploidy. The mean diameter of the megaspore (Figure 344), however, is 760 um which is large and suggests polyploidy. Similarly, *I. japonica* A. Br. and *I. philippinensis* Merrill & Perry, have small microspore lengths (30 um and 28um, respectively) and large megaspore sizes (both 540 um). *Isoetes taiwanensis* spore sizes are consistently small, however, with a mean microspore length of 24 um and a megaspore size of 365 um.

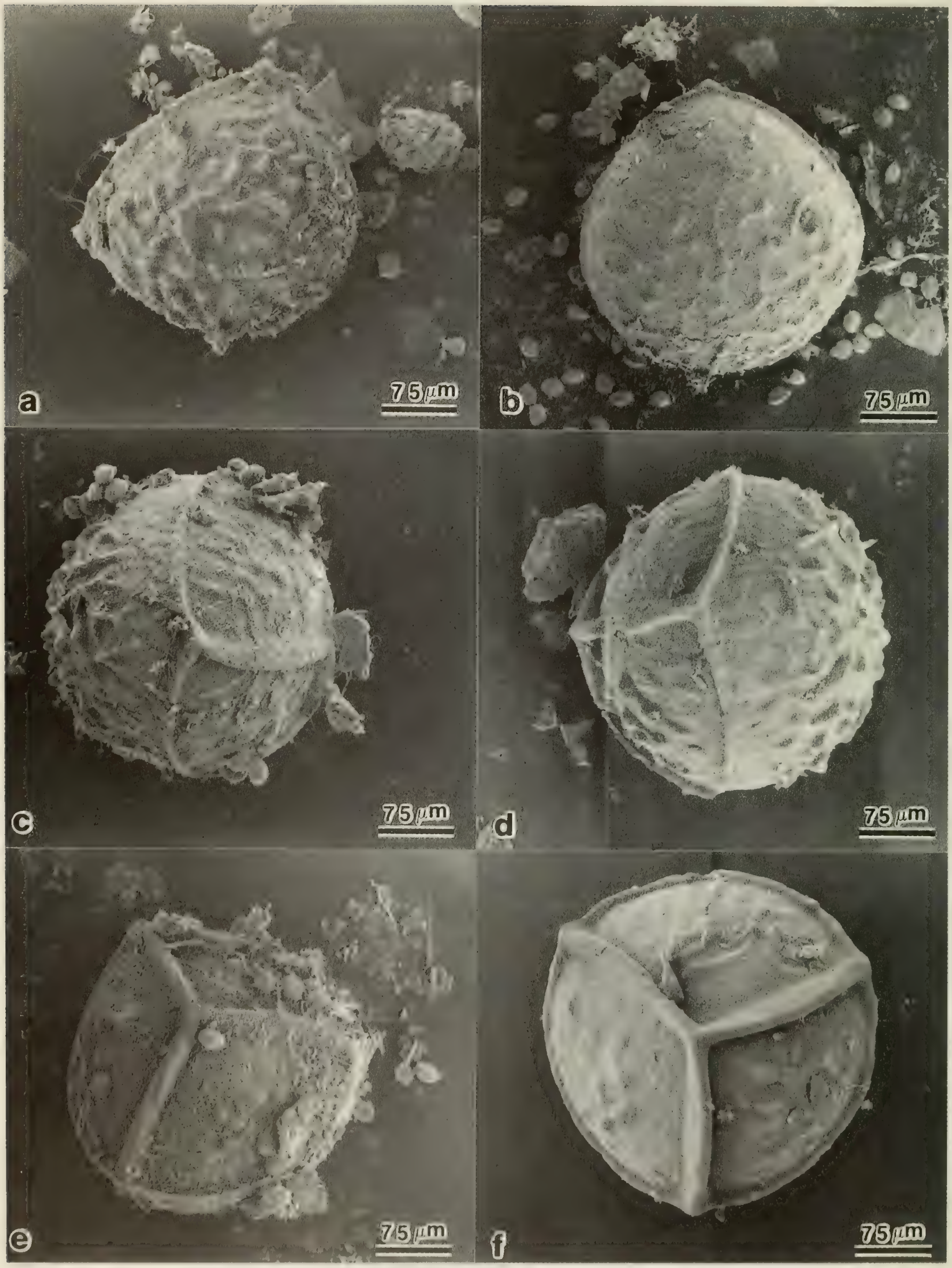

FIGURE 1: SEM micrographs of megaspores of *Isoetes taiwanensis.* 1a, 1c and 1e from Holotype, *Hsu 1715,* 1b from *Huang 6186,* 1d and 1f from *Huang and Yang 13557-7.* 1a and 1b are distal views, 1c and 1d lateral views and 1e and 1f are proximal or triradial views.

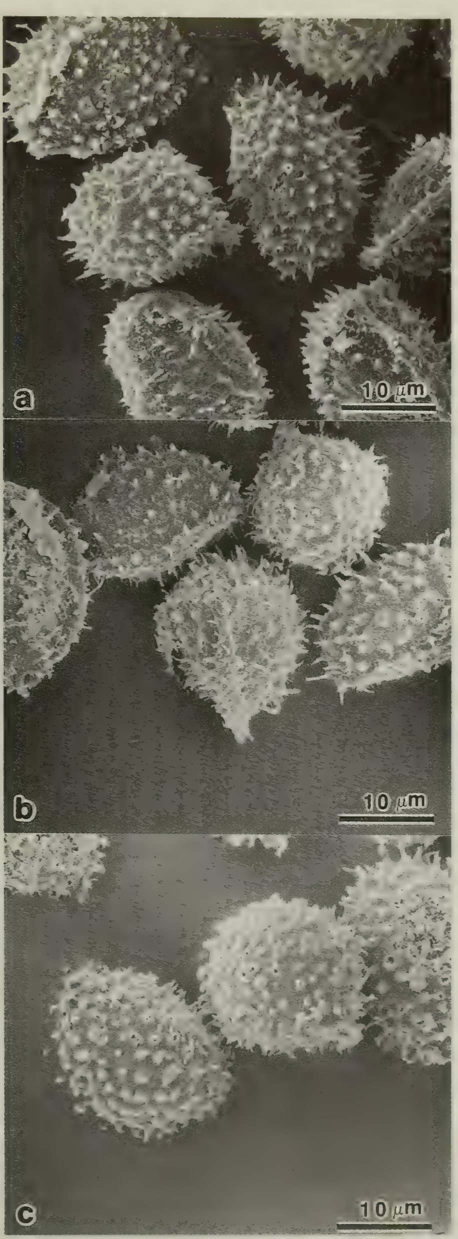

FIGURE 2: SEM micrographs of microspores of *Isoetes taiwanensis*. 2a from *Huang and Yang 13558-2*, 2b from *Huang and Yang 13557-7*, 2c from Isotype, *Hsu 1715*.

Clearly, there is a significant need for additional chromosome number determinations and for spore measurements to be made from cytologically determined specimens.

Affinities of *Isoetes taiwanensis*

Isoetes taiwanensis is a basic, sexual diploid which is endemic to a small, high elevation pond in northern Taiwan (De Vol 1972a). It lacks velum over its sporangia and has no specialized features in its leaves (De Vol 1972a, 1972b; Marsden 1979). We would place it close to *I. philippinensis* on the basis of geography and spore morphology, but the latter is probably a derived tetraploid since the megaspores are large (x= 54 µm). There are also some similarities in megaspore morphology between *I. taiwanensis* and *I. stevensii* Croft. The latter, an endemic of New Guinea, has low reticulations on the retate megaspores (Hickey 1986) and its spore sizes suggest that this is a derived tetraploid or hexaploid (microspores x= 37 µm, megaspores x= 550 µm).

We do not believe that *I. taiwanensis* is close to *I. japonica* A. Br. ssp. *japonica* of Japan which has large (500µm) megaspores with a highly developed "honeycomb" (reticulate) pattern and a 6x chromosome count (Yuasa 1935). Similarly, *I. sinensis* Palmer *(I. japonica ssp. sinensis* (Palmer) Marsden) of Japan and China is also not considered close to it on the basis of its large megaspores (x= ca. 410 µm) which suggest that it is likely a dervied tetraploid.

On ecological and geographic isolation criteria we would not look for a near relative of *I. taiwanensis* in Australia, especially in the southwest where most species are rock pool and terrestrial plants. The geographically remote Indian species with highly ornamented megaspores are also rejected as candidates.

Marsden (1979) grouped the *Isoetes* of his study area into six groups (Table 4, page 168). Groups I (echinate spores), III (Indian species with specialized megaspores), IV (derived polyploids) and VI (highly specialized Australian species) may all be rejected as having no possible basic, diploid sexual relatives close to *I. taiwanensis.* The remaining groups, then, are Group V (a 'catch-all' non-velate assemblage) and Group II (Velate). Marsden's (1979) catalogue of SEM photographs suggested several presumed diploid species that have similar or closely related spore morphologies to *I. taiwanensis.*

Marsden (1979) considered *I. taiwanensis* to be a member of the Group V complex of *Isoetes,* despite the fact that it is geographically and ecologically far removed from the remaining southern Australian rock pool and ephemeral wetland taxa in this group. He considered *I. drummondii* ssp. *drummondii* to be the closest of these taxa. *Isoetes drummondii* as treated by Marsden (1979), however, appears to included a number of taxa of ephemeral, disturbed sites across southern Australia which demonstrate ploidy levels between 2x and 6x. Some spores [e.g. microspores (Figure 241-242) and, to a lesser degree, megaspores (Figure 121) in Marsden (1979)] look similar to those of *I. taiwanensis* but it is impossible to know which relate to diploid populations and which are polyploids. In any event, the ecological, geographic and megaspore differences argue against *I. drummondii* in part or in whole, being a close relative of *I. taiwanensis.* The other possibly diploid members of Marsden's Group V that we have considered (and rejected) are:

- *I. attentuata* Marsden – similar microspores (Figure 279 of Marsden 1979) but with megaspore ornamentation closer to *I. coromandelina L. f.;* a single-site, ephemeral swamp endemic of southern Australia;
- *I. caroli* Johnson – similar megaspores (Figures 143 of Marsden 1979) but with fibrously-tubercled microspores (Figures 292 of Marsden 1979) very different from *I. taiwanensis;* a southwestern Australian endemic of ephemeral rock pools;
- *I. brevicula* Johnson – similar megaspores (Figures 69-70 of Marsden 1979); microspores not illustrated; a tiny endemic of ephemeral rock pools in southwestern Australia.

Three possibly diploid species in Group II were considered as possible close relatives of *I. taiwanensis* despite their velate characteristics, *I. pusilla* Marsden, *I. muelleri* A. Br. and *I. kirkii* A. Br. *Isoetes pusilla* is unlikely because of its differing spores, with highly developed lattice ornamentation on the megaspores (Figures 145-147) and the sparsely-spined microspores (Figures 251-252), and its geographic isolation as a southeastern Australian endemic (Marsden 1979). *Isoetes muelleri* represents the same set of problems as *I. drummondii, viz.* similar megaspore morphology in some cases (Figures 100 and 111 - Marsden 1979), varying cytological information (counts indicating populations with ploidy levels of 2x to at least 5x) and geographic confinement to Australia. In addition, the microspores illustrated in Marsden (1979) are compeltely unlike those of *I. taiwanensis.*

The most likely choice for closest affinity to *I. taiwanensis* appears to be *I. kirkii (s. st.),* an endemic of geologically young, lower elevation volcanic lakes on the North Island of New Zealand. This diploid not only occupies a similar habitat to that of *I. taiwanensis,* it demonstrates a close similarity in ornamentation of megaspores (Figures 81-86 (though certainly not the distal view of Figure 88 with many pustules) and microspores (Figures 273-274) (Marsden 1979). The other New Zealand diploid endemic, *I. alpinus* Kirk, is similar to *I. kirkii* (recently treated as *I. kirkii* var. *alpinus* (Kirk) Marsden & Chinnock) but has mostly unornamented megaspores (Figures 73-75, Marsden 1979) and is largely confined to oligotrophic glacial lakes at higher elevations on the South Island (Brownsey and Smith-Dodsworth 1989; Jolly and Brown 1975).

This analysis leads to the speculative conclusion when emphasizing diploidy, spore morphlogy and ecology that *I. taiwanensis* is a part of a complex of cold water, high elevation, island species that extends today from Taiwan *(I. taiwanensis)* to New Zealand *(I. kirkii* and *I. alpinus),* with derivative polyploids *I. philippinensis* and *I. stevensii* (and the other New Guinea species ?). Also from this anccestral stock *I. brevicula* and *I. caroli* would be specialized derivatives adapted to granite rock knob pools confined (at least now) to southwestern Australia. Our analysis also suggests that Marsden's (1979) Groups are artificial and may confuse understanding of biological affinities within the genus in this area.

Polymorphic spores and hybridity

Marsden (1976b, 1979) classified megaspores into categories of Type I, Type IIa, IIb and Type III. Type I megaspores are monomorphic spores from species typical of sexual diploid taxa and sexual alloploids. The other types are examples of the consequences of disturbed meiosis, together with variable or a lack of cytokinesis (Jeffrey 1937). Type III spores are particularly striking, with "bridged" or dumb-bell shaped spores and giant spores ("basketball" spores) which are monolete, not the expected trilete. We have studied polymorphic spores and Type III spores in material from North America and we consider that these are excellent indicators of hybrids (Taylor and Luebke 1988; Britton and Brunton 1989; Britton 1991; Brunton and Britton 1991).

Although no hybrid *Isoetes* has been reported from the southern hemisphere we believe that a number of the SEM photographs in Marsden (1979) illustrate undescribed hybrids. A particularly strong argument can be made in case of *I. drummondii* var. *anomala* Marsden of southern Australia. It apparently is pentaploid (5x), it lacks microspores and it has Type III spores – all indicative characteristics in known *Isoetes* hybrids (Britton and Brunton 1989; Brunton and Taylor 1990; Britton and Brunton 1991; Brunton and Britton 1991). Unfortunately, more definitive analysis is hampered by inconsistencies in the data presented in Marsden (1979). Variety *anomala* is described as "consistently" 5x in the text (page 92) but is cited on the chart on page 51 as 4x or 5x. Curiously, the 4x count is given as "this study" and the 5x from his 1973 honours thesis, citations which appear reversed. Also, although *I. drummondii* var. *drummondii* is cited as a diploid, microspore size (25 to 35 µm) suggests that populations with higher ploidy are involved. Microspore morphology as shown in Figures 237-242 is also unusually variable. Much the same is evident with megaspore sizes (250 to 550 µm). We feel there may be an undescribed allotetraploid hidden in this complex. The pentaploid var. *anomala* could be the result of a cross of the undescribed 4x (unreduced) x 2x *drummondii,* although a wider cross is not ruled out.

CONCLUSIONS

Isoetes taiwanensis a unique, rare, endemic species with distinctive spores in comparison with the 29 species of Marsden (1979) appears to be a member of a complex of cold water, high elevation island species with retate to tuberculate megaspore ornamentation which occur along the western Pacific rim from Taiwan to New Zealand.

More cytological determinations are needed from which microspore and megaspore measurements can be made. These will be of critical value to more definitive taxonomic and evolutionary studies. The SEM catalogue of spores will also have more value when it is based on cytologically determined material. Although Marsden (1979) shows a wealth of variation in the SEM pictures of spores it is difficult to determine the frequency of particular morphologies and which constitutes the norm.

We feel that basic, sexual diploid *Isoetes* species should be well studied before extrapolating to polyploids, apomicts and hybrid derivatives. Only then will a satisfactory taxonomic system based on the concept of biological species be possible for the *Isoetes* of the Australasia, India and the western Pacific area.

ACKNOWLEDGEMENTS

The authors would like to thank Professor B. C. Lu of Guelph for his initial enquiry to C. C. Chen, National Taiwan University, concerning our loan from TAI. We also thank Debbie Blair for obtaining the SEM pictures. We appreciate the continued support of NSERC to the senior author for this study.

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The following four Figures in *Gazette* 14(1) pages 20 & 21 inadvertently did not have their bar-scales. They are here repeated complete.

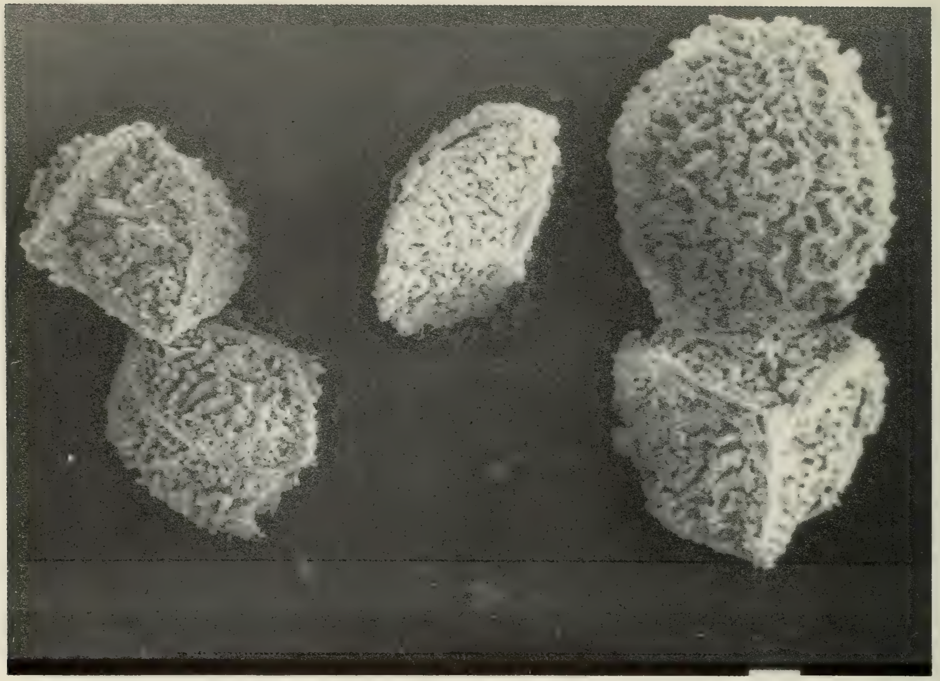

FIGURE 1: Megaspores of *I.* × *hickeyi* (Brunton 9327A (OAC), Bar = μm). Note variable size, distorted shape and irregular surface ornamentation typical of *Isoetes* hybrids.

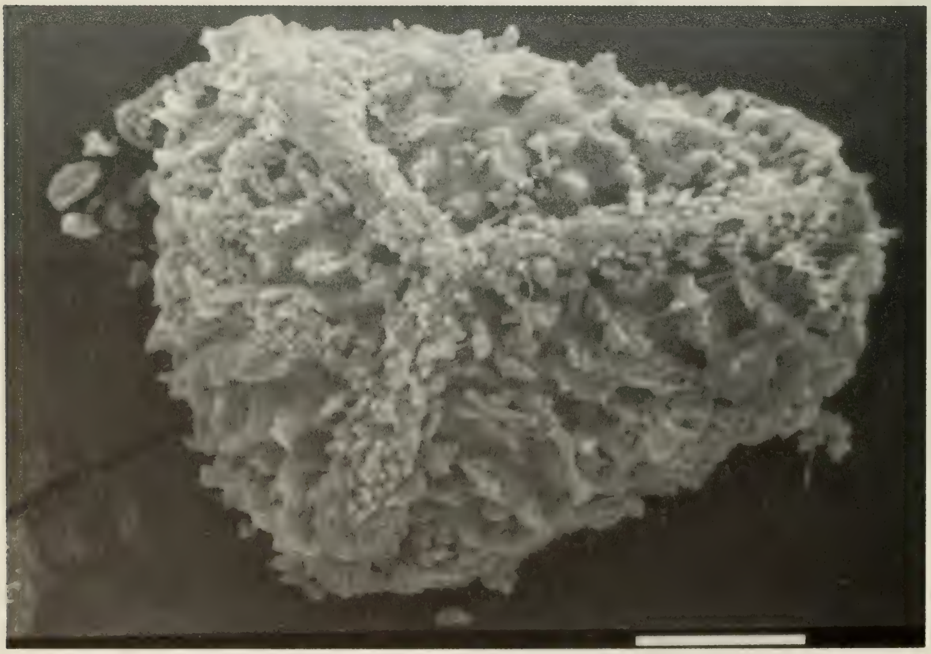

FIGURE 2: SEM photomicrograph of triradial hemisphere of *Isoetes* × *hickeyi* megaspore (Brunton 9327A (OAC), Bar = 100μm).

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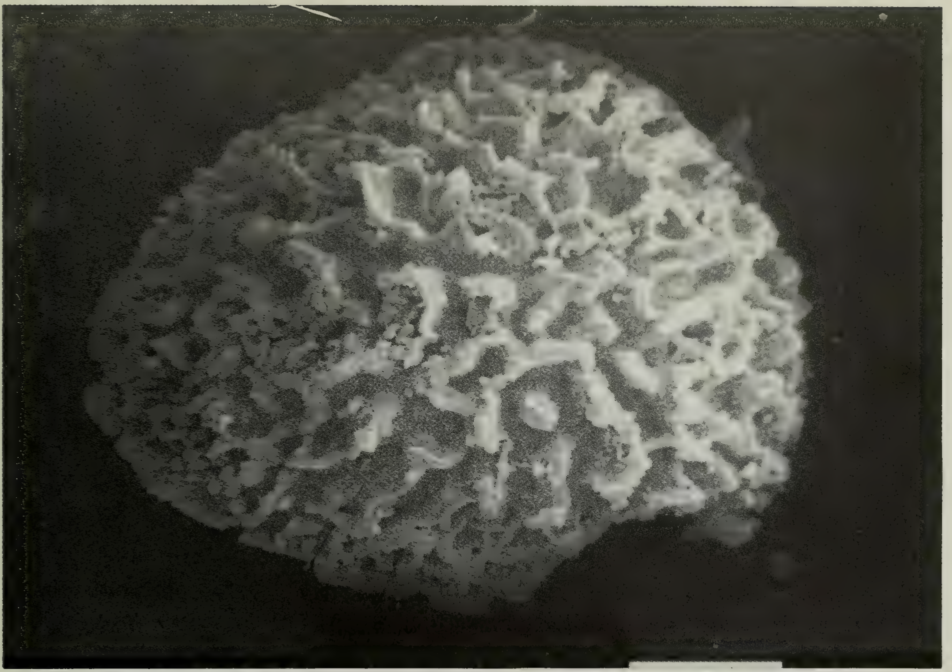

FIGURE 3: SEM photomicrograph of distal hemisphere of *Isoetes* × *hickeyi* megaspore (Brunton 9327A (OAC), Bar = 100 µm). Note narrow band of papillae by the equator.

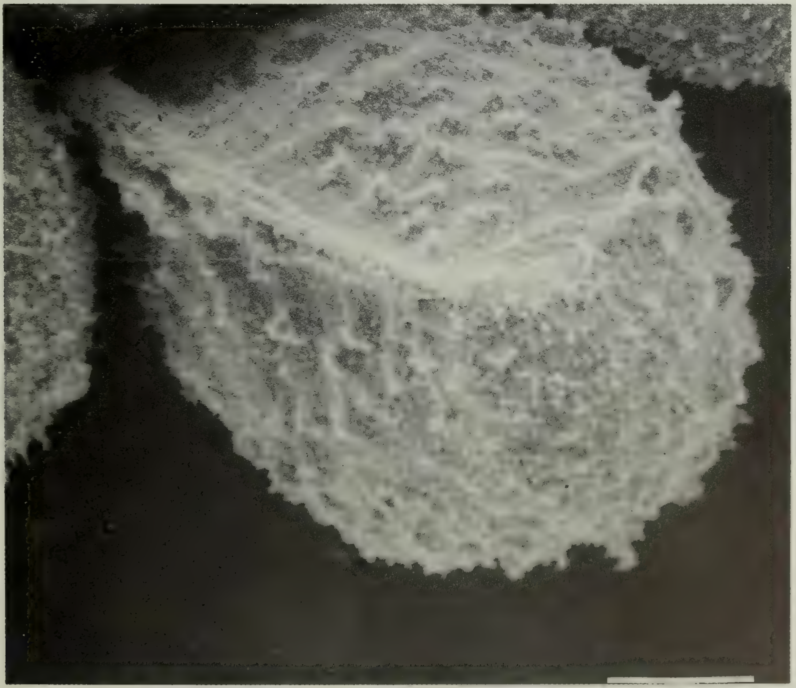

FIGURE 4: SEM photomicrograph of microspore of *Isoetes* × *hickeyi* (Di Labio, s.n. (OAC), Bar = 11 µm).

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THE FERN GAZETTE

VOLUME 14 PART 2 **1991**

CONTENTS

Page

MAIN ARTICLES

Curl-tip disease of *Pteridium aquilinum* (Dennstaedtiaceae: Pteridophyta)
- J.A. Irvine, M. McElwee & M.N. Burge 41

Allelopathy in bracken *Pteridium aquilinum* (Dennstaedtiaceae: Pteridophyta)
- I.N. Josephine Storey 51

***Anogramma leptophylla* (Sinopteridaceae: Pteridophyta) an aneuploid taxon?**
- F.J. Pérez Carro & Ma P. Fernández Areces 55

The palaeobotanical case for dividing *Selaginella* (Selaginellaceae: Pteridophyta)
- Barry A. Thomas & Nat Quansah 59

The systematic status of *Matteuccia intermedia* (Woodsiaceae: Pteridophyta)
- M. Kato, T. Suzuki & N. Nakato 65

The spores and affinities of *Isoetes taiwanensis* (Isoetaceae: Pteridophyta)
- Donald M. Britton & Daniel F. Brunton 73

SHORT NOTES

The Malesian pteridophytes of Raciborski
- P.S. Köhler 50

***Acrostichum aureum:* an inland record from Saudi Arabia**
- I.S. Collenette 57

CORRIGENDA 72, 82

NOTES FOR CONTRIBUTORS, ETC. 84

REVIEWS

South African Ferns and Fern Allies 50

Proceedings of the International Symposium on Systematic Pteridology 54

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A REVISED LIST OF THE PTERIDOPHYTES OF NEVIS

B M GRAHAM
Polpey, Par, Cornwall PL24 2TW

M H RICKARD
The Old Rectory, Leinthall Starkes, Ludlow, Shropshire SY8 2HP

ABSTRACT

A revised list of the pteridophytes of Nevis in the Lesser Antilles is given. This includes 14 species not previously recorded for the island.

INTRODUCTION

Nevis is a small volcanic island in the West Indian Leeward Islands. No specific list of the ferns has ever been published, although Proctor (1977) does record each of the species known to occur on the island. Proctor's records were largely accumulated from herbarium specimens collected by R A Howard in 1950 and his own collections in 1959. In total he recorded 81 taxa. Collections by one of us (BMG) in 1988 and both of us in 1990 have added a further 14 species plus 3 unnamed species of *Thelypteris* and 4 established garden introductions. Nineteen species recorded in *Proctor* were not seen by either of us on the island. The 98 native or naturalised taxa here recorded for Nevis are still low in comparison with the number recorded for the two larger principal neighbouring islands of St Kitts: 129 (Proctor 1977) and Monserrat: 117 (Proctor 1977).

Nevis is approximately 6 miles from east to west and 8 miles from north to south, a total surface area of 36 square miles. The whole island is dominated by the central mountainous core rising to 3,232 feet at Nevis Peak. About 9,000 people live on the island mostly around the coastal plain and especially in the west near Charlestown, the Capital. The central mountainous area is unpopulated and rarely visited by the local inhabitants.

The climate is tropical with the temperature rarely falling below 20°C. The prevailing winds blow from the south east with most rainfall at high altitudes (more than 100 inches annually), particularly to the north west of the summit peak. Here, cloud frequently hangs all day in the remnants of the summit crater protected from the prevailing winds and occasional hurricanes, e.g. hurricane Hugo in 1989. Rainfall is low (less than 40 inches annually) in southern and eastern coastal areas where semi-desert scrub has developed.

Rodriques (1990) has mapped the vegetation of the island (see Fig. 1) and found that less than 4 square miles (624 hectares) of montane type forest exists on Nevis. He has further subdivided this area into three zones:- Montane forest – 500 hectares, Palm break – 115 hectares, Elfin forest – 9 hectares.

Montane forest would be at an altitude of about 1500-2300 feet, palm brake from 2300-2700 feet and the elfin forest from 2700-3232 feet. At the time of the 1990 collecting much of this forest, especially on the windward side of the island, was still recovering from the damage caused by hurricane Hugo.

Low altitude species – less than 1000 feet

There are few ferns naturally occurring below 1000 feet. Exceptions are *Acrostichum danaefolium* in mangrove swamps at sea level, and ferns of walls and dry rocky areas, e.g. *Cheilanthes microphylla*, *Anemia adiantifolia*, *Pteris vittata* and *Pityrogramma calomelanos*.

Middle altitudes in dry evergreen forest – 1000-1500 feet

In sheltered areas several species tolerant of temporary drought are abundant, eg. *Blechnum*

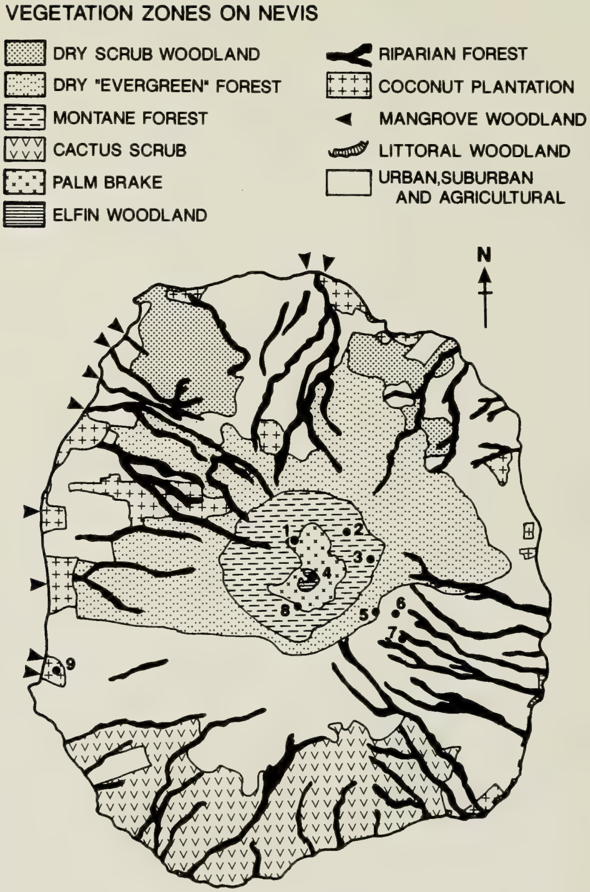

FIGURE 1. Vegetation zones of Nevis (after Rodriques, 1990).

occidentale, Nephrolepis rivularis, Selaginella flabellata and on trees and rocks *Polypodium polypodioides, Polypodium aureum* var. *aureum* and *Polypodium lycopodioides.*

Montane forest – 1500-2300 feet

Here tree-ferns are common, usually *Cyathea muricata* and *C.arborea*, but occasionally in more sheltered areas at higher altitudes the much smaller *Cnemidaria grandifolia* var. *grandifolia* is frequent. The ground vegetation is rich in ferns with *Diplazium spp., Tectaria incisa, Lonchitis hirsutus* and many *Thelypteris* species locally dominant. The striking red young fronds of *Adiantum latifolium* are frequent in forest clearings and a problematical taxon, probably also *A. latifolium*, occurs occasionally on rocks.

In sheltered valleys on tree trunks and where rocks outcrop many species of filmy fern occur. Particularly common are *Trichomanes membranaceum* and *Trichomanes alatum.* Also on rocks, but in more open sites, *Asplenium laetum, A. abscissum* and *A. cristatum* occur occasionally, with in one collection a problematical frond which might possibly be *A.malcolm-smithii* – believed endemic to St Kitts. *Lomariopsis sorbifolia, Grammitis serrulata, Thelypteris reptans* var. *reptans*, several polypodiaceous species and *Vittaria lineata* also grow occasionally on rocks and trees.

Dominant flowering plants include (after Rodriques, 1990) *Sloanea truncata, Miconia spp, Dacryodes excelsa, Euterpe globosa, Beilschmeida pendula, Coccoloba pubescens, Aniba bracteata, Simarouba amara, Ceropia peltata* and *Podocarpus coriaceus.*

Palm brake – 2300-2700 feet

In this zone several species of palm are particularly common, dicotyledonous trees also occur as do many ferns, although none appear to be restricted to the palm break. All three tree-fern species occur, *Hymenophyllum hirtellum* subsp. *gratum* is abundant on many moss festooned trees together with *Trichomanes alatum* and *T. crispum*. Also frequent are *Polypodium loriceum* and *Grammitis seminuda*.

Dominant species of flowering plants (after Rodriques, 1990) are *Euterpe globosa* and *Podocarpus coriaceus*.

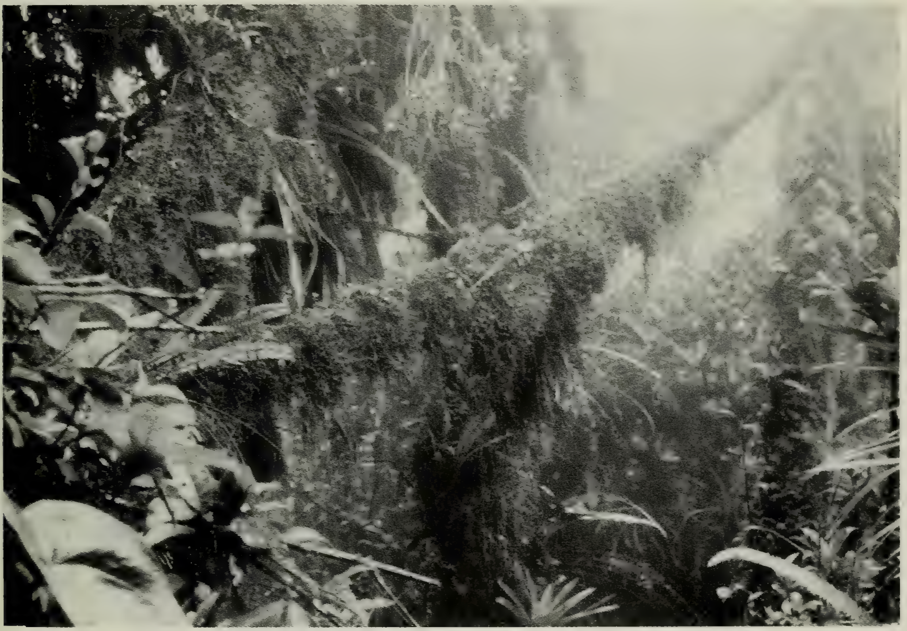

FIGURE 2. Moss festooning branches in elfin forest.

Elfin forest – 2700-3232 feet

This zone is the jewel in the crown (See Figs. 2 & 3). In an area perhaps only extending to 9 hectares several of the more interesting species are abundant. *Gleichenia furcata* tangled with *Dicranopteris pectinata* swamp many of the more exposed ridges and invade to some extent the tiny areas of summit heaths where *Lycopodium cernuum* var. *dussii* is common. In the dense almost impenetrable forest all branches, creepers and tree trunks are thickly festooned with mosses, bromeliads and ferns. There appear to be no rock faces as such and species from genera normally considered epipetric are common in these festoons, eg *Hymenophyllum elegans, Grammitis serrulata, G. flabelliformis* and *G. suspensa*. Particularly conspicuous among these epiphytic ferns is *Blechnum binervatum* with its arching fronds, spiralling from the thick scaley rhizomes, climbing around the stems of *Cyathea arborea*. Also magnificent is the terrestrial *Thelypteris decussata* with fronds up to 3 metres in length. *Blechnum ryanii* and *Cnemidaria grandifolia* var. *grandifolia* are abundant, while growing on the dark forest floor *Lindsaea quadrangularis* subsp. *antillensis* and *Trichomanes trigonum* var. *trigonum* are frequent. The fronds of this filmy fern grow erect to a height of 30 or 40 cm and are remarkably tough despite their filmy nature. Less spectacular, but of greater significance, is *Thelypteris muscicola* which occurs only rarely right at the summit of Nevis Peak. This species grows nowhere else in the world.

Dominant species of flowering plants (after Rodriques, 1990) are *Euterpe globosa, Ficus sp., Clidemia umbrasa* and *Podocarpus coriaceus*.

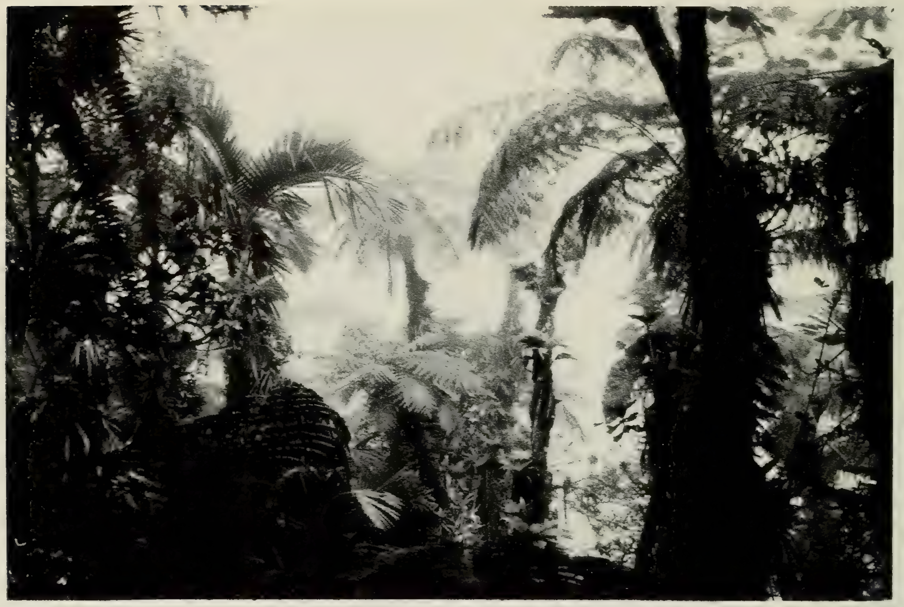

FIGURE 3. *Cyathea arborea* dominating the elfin forest at the summit.

SPECIES LIST

Most determinations have been confirmed by Dr Dennis Adams. Species recorded in Proctor (1977) have been incorporated to give a list of the ferns of Nevis as comprehensive as possible at the present time. Order and nomenclature is usually as in *Flora of the Lesser Antilles - Pteridophyta* (1977) by G R Proctor. Where different, old names are given in brackets. Common names are taken from Jones (1987). Entries of introduced species are preceded by an *. Heights, given in feet, are taken from the map of the island published by the Government of the United Kingdom (Ordnance Survey) for the Government of St Kitts and Nevis (1984).

Representative ranges of herbarium specimens have been placed at the National Museum of Wales, Cardiff (NMW), and the Natural History Museum, London (BM). The numbers are given in the following list. MHR/BMG number is followed by (BM) and/or (NMW + number), eg. 191(BM);192(NMW.V91.115.41).

Psilotum nudum (L.) Griseb. Whisk Fern. Walls on Golden Rock Estate, c.900 feet, 1988 and 1990, 338(NMW.V91.115.72).

Lycopodium taxifolium Sw. Mossy stumps and trunks or branches of trees in moist forests at middle to high elevations. Proctor (1977).

Lycopodiun cernuum L. var. *cernuum*. Nodding Clubmoss. In grassy area at margin of track to the Source, c.1400 feet, 1990, 191(BM);192(NMW.V91.115.41). **New record**

Lycopodium cernuum L. var. *dussii* Christ. Open areas at high altitude. Above Tower Hill, c.2800 feet, 1990, 531 (NMW.V91.115.75). Summit heath, 3100-3232 feet, 1990, 185(BM); 188(NMW.V91.115.40). (Fig. 4).

Selaginella flabellata (L.) Spring. Very common in forest from c.1000-2000 feet, 1988/90. Route to Source, 1990, 198(NMW.V91.115.42).

Selaginella substipitata Spring. Common at moderate to high altitudes, c.2000-3200 feet. Nevis Peak, 1990, 194(BM); 212(NMW.V91.115.44).

Selaginella serpens (Desvaux) Spring. Frequent in dense forest towards summit, 3000-3200 feet, 1990, 206(NMW.V91.115.43). **New record.**

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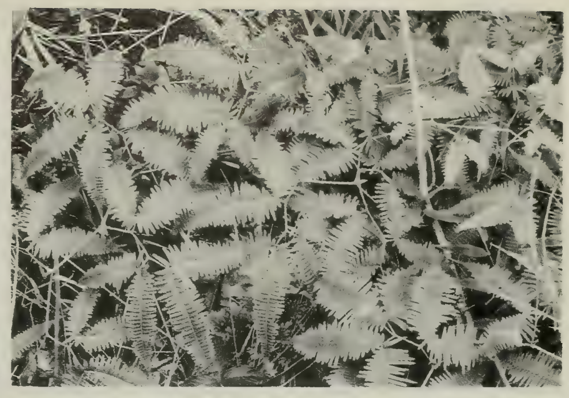

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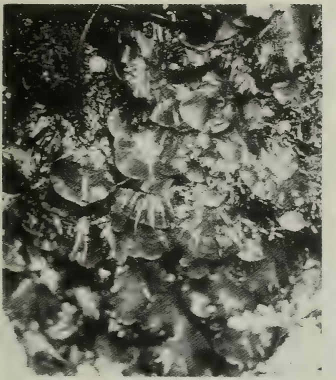

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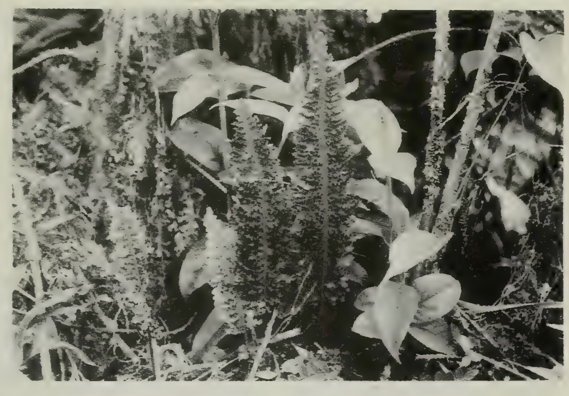

FIGURE 4. *Lycopodium cernuum* subsp. *dussii* in summit heath.
FIGURE 5. *Dicranopteris pectinata* in open area on summit ridge.
FIGURE 6. *Trichomanes membranaceum*.
FIGURE 7. *Trichomanes trigonum* var. *trigonum* in elfin forest.

Anemia adiantifolia (L.) Sw. Pine Fern. Walls at Golden Rock 1988 and 1990 at c. 800 feet, 347(BM); 348(NMW.V91.115.76). Rawlins village, c.900-1200 feet, 1988/90. **New record.**

Dicranopteris pectinata (Willd.) L.M.Underw. Open sites and in forest margins on summit ridges, c.2800-3230 feet. Nevis Peak, 1990, 53(BM); 42(NMW.V91.115.11). **New record.** (Fig. 5).

Gleichenia furcata (L.) Sprengel. Open sites and in forest margins on summit ridges. Above Tower Hill, 2700-2800 feet, 1990. Summit at 3230 feet, 1990, 50(NMW.V91.115.12).

Hymenophyllum lineare (Sw.) Sw. Mossy tree trunks at higher elevations, Proctor (1977).

Hymenophyllum elegans Sprengel. Cloud forest at summit of Nevis Peak, 3220 feet, 1990, 286(BM); 284(NMW.V91.115.57).

Hymenophyllum hirsutum (L.) Sw. Mossy logs and tree trunks at chiefly middle elevations, Proctor (1977).

Hymenophyllum hirtellum Sw. var. *gratum* (Fée) Proctor. Common in forest epiphytic on trees. Above Tower Hill from 1600-2800 feet, 1990, 303(BM); 298(NMW.V91.115.60). Summit at c.3220 feet, 1990, 307(NMW.V91.115.61).

Hymenophyllum macrothecum Fée. On fallen tree at Source, c.1600 feet, 1990, 295(NMW.V91.115.59).

Hymenophyllum polyanthos (Sw.) Sw. var. *polyanthos*. Common in vicinity of Source on rocks and trees, c.1600 feet, 1988 and 1990, 289(NMW.V91.115.58). Also on summit ridge above Tower Hill, c.2800 feet, 1990.

Trichomanes hymenophylloides van den Bosch. Vicinity of Source, c.1600 feet. 1988 and 1990, 217(BM); 218(NMW:V91.115.45); 221(NMW.V9.115.46). Also above Tower Hill, c.1700 feet, 1990.

Trichomanes rigidum Sw. Rare on rocks in ravine near Source, c.1600 feet, 1990, 222(BM); 226(NMW.V91.115.47). **New record**.

Trichomanes membranaceum L. Abundant on rocks and tree trunks along route to Source and at Source, c.1600 feet, 1988 and 1990, 248(BM); 249(NMW.V91.115.52). (Fig. 6).

Trichomanes punctatum Poiret in Lam. Abundant on rocks and tree trunks. On rocks in ghut east of Tower Hill, c.1200 feet, 1990. On route to Source and at Source, c.1600 feet, 19888 and 1990, 237(NMW.V91.115.49).

Trichomanes angustifrons (Fée) Wessels Boer in Kramer. At Source, rare, c.1600 feet, 1990, 239(NMW.V91.115.50).

Trichomanes krausii Hook. & Grev. On rocks on route to Source, rare, c.1600 feet, 1990, 228(BM); 230(NMW.V91.115.48). **New record**.

Trichomanes trigonum Desvaux var. *trigonum*. In forest usually at higher altitudes. Above Tower Hill, c.1700 feet, 1990, 277(NMW.V91.115.55). Common near summit of Nevis Peak growing on forest floor, 2800-3230 feet, 1990, 278(BM). (Fig. 7).

Trichomanes polypodiodes L. In forest above Tower Hill, c.1700 feet, 1990, 280(NMW.V91.115.56).

Trichomanes alatum Sw. Very common in forest, on rocks, trees or on forest floor. Source and route to Source, c.1600 feet, 1988 and 1990, 270(BM); 255(NMW.V91.115.53), 265(NMW.V91.115.54). Above Tower Hill, 1700-2700 feet, 1990, 254 (BM).

Trichomanes crispum L. Rocks on route to Source, c.1600 feet, 1988 and 1990, 241(BM). Damp forest along ridge above Tower Hill, 1700-2600 feet, 1990, 246(NMW.V91.115.51), 516(NMW.V91.115.105).

Cyathea muricata Willd. in L. Common at middle altitudes in forest. Route to Source, c.1400-1600 feet, 1988 and 1990, 380,388,500(BM); 385(NMW.V91.115.81), 387(NMW.V91.115.82), 501(NMW.V91.115.103). Forest above Tower Hill, 1500-2500 feet, 1990.

Cyathea arborea (L.) Smith. West Indian Tree-fern. In forest at slightly higher altitudes than previous species. Route to Source, c.1600 feet, 399,498(BM); 391,398,400(NMW.V91.115.83), 499(NMW.V91.115.102). Near Source, c.1700 feet, 1990. Forest from c.1600 feet to summit at 3230 feet, 1990. (Fig. 8).

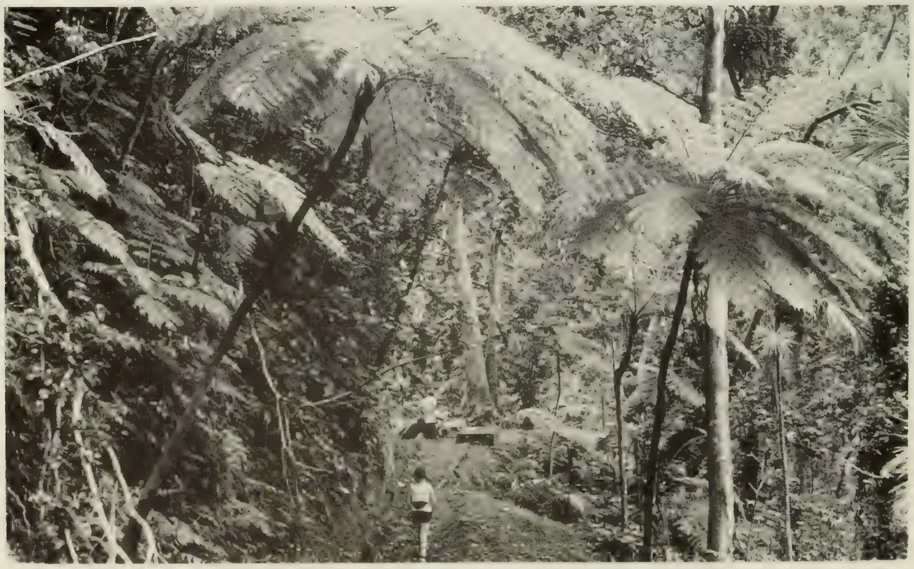

FIGURE 8. *Cyathea arborea* in montane forest.

Cnemidaria grandifolia (Willd.) Proctor var. *grandifolia*. Abundant in very damp sheltered forest at middle to high altitudes. Above Tower Hill, 1600-2800 feet, 1990, 409,413,415(NMW.V91.115.86). Above Zetlands, c.1800 feet, 1990. Summit cloud forest c.3230 feet, 1990.

Lindsaea quadrangularis Raddi subsp. *antillensis* Kramer. Occasional on forest floor in damp forest at moderate to high altitudes. Above Tower Hill, 2400-2700 feet, 1990, 479(NMW.V91.115.99). Summit forest 3230 feet.

Lonchitis hirsuta (L.) (*Anisorus hirsutus* (L.) Underw. & Maxon). In damp sites alongside route to Source, c.1600 feet, locally common, 1988 and 1990, 345(BM); 342,346(NMW.V91.115.74). (Fig. 9).

Pteris vittata L. Chinese Brake. Just above sea level to 1000 feet on walls and rockwork. Walls in Charlestown, 1990. Golden Rock Estate, even colonising crevices in concrete by swimming pool c.900 feet, 1988 and 1990, 325(BM);327(NMW.V91.115.68).

Pteris altissima Poiret in Lam. Forest Brake. Occasional in lower altitude forest on banks above streams. Bank above Source reservoir, c.1700 feet, 1990, 322(NMW.V91.115.67). Bank of ghut above Tower Hill, c.1200 feet.

Acrostichum danaeifolium Langsd. & Fischer. Giant Leather Fern. Saline or brackish swamps, Proctor (1977).

Blechnum occidentale L. Hammock Fern. Abundant in dryer forest at lower altitudes. Route to Source, 1200-1500 feet, often dominant, 1988 and 1990, 98(NMW.V91.115.21). Above Tower Hill, c.1200-1500 feet, 1990. Above Zetlands, 1990. Golden Rock Estate in dry forest, c.850 feet, 1988. (Fig. 10). Form with forked pinnae also common along route to Source, 1990, 101(NMW.V91.115.22).

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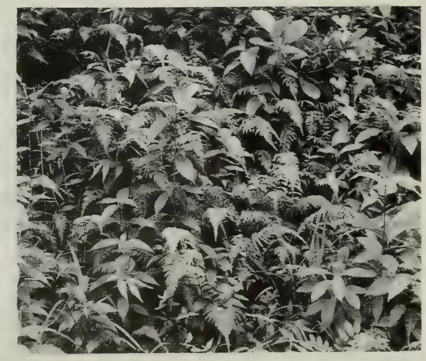

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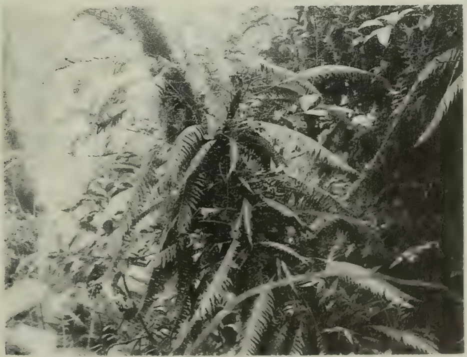

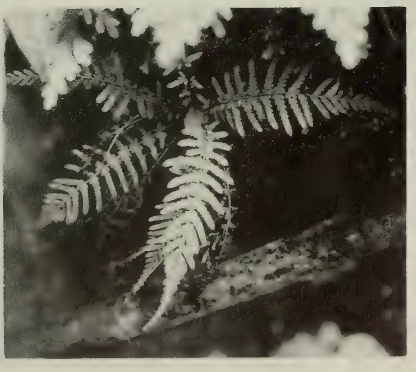

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FIGURE 9. *Lonchitis hirsuta*.
FIGURE 10. *Blechnum occidentale*.
FIGURE 11. *Blechnum binervatum* in elfin forest.
FIGURE 12. *? Thelypteris sancta* near Source.

Blechnum binervatum (Poiret) Morton & Lellinger. Common on trunks of *Cyathea arborea* in cloud forest at summit, 3150-3230 feet, 1990, 103,110(BM); 106(NMW.V91.115.23), 109(NMW.V91.115.24). **New Record**. (Fig. 11).

Blechnum insularum Morton & Lellinger. Mossy montane forests at higher elevations, Proctor (1977).

Blechnum ryanii (Kaulf.) Hieron. Common in cloud forest at high altitudes. Above Tower Hill at c.1600 feet, 1990, 112,113((BM). Summit forest 3200 feet, 1990, coll. Q.Henderson, 114(NMW.V91.115.25).

Pityrogramma calomelanos (L.) Link. Silver Fern. Common from just above sea level to c. 1600 feet on rocks and walls. Route to Source, c.1600 feet, 1988 and 1990, 36(NMW.V91.115.84). Golden Rock Estate, common on walls, 1988 and 1990, 39(BM); 38(NMW.V91.115.10). Charlestown, 1990. **New record**.

Pityrogramma chrysophylla (Sw.) Link. Uncommon on rocky bank. Route to Source, c.1600 feet, 1900, 35(NMW.V91.115.09).

Cheilanthes microphylla (Sw.) Sw. Dry walls. Route to Golden Rock, c.700 feet, 1988 and 1990, 333(BM); 336(NMW.V91.115.71). Gingerland, 650 feet, 1990.

Adiantum caudatum* L. Trailing Maidenhair. Not native, semi-naturalised Golden Rock Estate. c.850 feet, 1988 and 1990, 63(NMW.V91.115.14). **New record.

Adiantum latifolium Lam. Partly shaded banks, borders of pastures and alluvial thickets at low to middle elevations. (Proctor 1977). Route to Source, 1400-1700 feet 1988 and 1990, 69(BM); 70(NMW.V91.115.15), 74(NMW.V91.115.16). Above Tower Hill, c.1700 feet, 1990. (Det. A C Jermy).

Adiantum tetraphyllum Humb. & Bonpl. ex Willd. in L. Partly shaded banks, borders of pastures and alluvial thickets at low to middle elevations, Proctor (1977).

Adiantum tenerum Sw. Common at foot of shady banks. Golden Rock Estate, 850 feet, 1988 and 1990, 58,59(NMW.V91.115.13). Rawlins village, 100 feet, 1990, 54(BM).

Elaphoglossum petiolatum (Sw.) Urban. Tree branches. Route to source c.1600-1700 feet, 1990, 365(NMW.V91.115.79). Above Tower Hill, c.1700 feet, 1990.

Elaphoglossum schomburgkii (Fée) T. Moore. Shaded mossy ledges, stumps and trees at middle to higher elevations, Proctor (1977).

Elaphoglossum impressum (Fée) T. Moore. Trees at Source, 1700 feet, 1990, 363(BM);364(NMW.V91.115.78).

Elaphoglossum martinicense (Desvaux) T. Moore. Trees. Route to Source and Source, c.1600 feet, 1990, 371(BM); 370(NMW.V91.115.80). Above Tower Hill, c.1700 feet.

Elaphoglossum plumieri T. Moore. On mossy tree trunks at chiefly higher elevations, Proctor (1977).

Elaphoglossum apodum (Kaulf). Schott. On mossy tree trunks, rarely on mossy banks or ledges, at middle to higher elevations, Proctor (1977).

Hymenodium crinitum (L.) Fée. Elephant Ear Fern. On mossy tree trunks, rarely on rocks, at chiefly middle elevations, Proctor (1977).

Lomariopsis sorbifolia (L.) Fée. Climbing on rocks and trees at lower altitudes in forest. On rocks in vicinity of Source, c.1600 feet, 1988 and 1990, 331(BM); 330(NMW.V91.115.70). On trees by side of ghut east of Tower Hill, c.1200 feet, 1990. **New record**.

Olfersia cervina (L.) Kunze (*Polybotrya cervina* (L.) Kaulf.). Common alongside route to Source, c.1600 feet, 1988 and 1990, 340(BM – fertile frond); 341(NMW.V91.115.73).

Nephrolepis rivularis (Vahl). Chr. Abundant in forest from 1000-3230 feet. At summit, 17(NMW.V91.115.04). Equally common in open glades and cloud forest. Also in gardens, eg Golden Rock, 1988 and 1990, 14(NMW.V91.115.03).

**Nephrolepis hirsutula* (Forst.) C. Presl cv. 'Superba'. Established in gardens, eg Golden Rock, c.850 feet, 1988 and 1990, 21(NMW.V91.115.05).

**Nephrolepis falcata* (Cav.) C. Chr. cv. 'Furcans'. Fishtail Fern. Golden Rock garden, c.850 feet, 1988 and 1990, 26(NMW.V91.115.06).

**Nephrolepis cordifolia* (L.) Presl. cv. 'Duffii'. Golden Rock garden, c.850 feet, 1988 and 1990, 28(NMW.V91.115.07).

Tectaria plantaginea (Jacq.) Maxon. On rocks and clay banks in moist, deeply shaded ravines, or occasionally on floor of tall primary rain forest, at chiefly middle elevations, Proctor (1977).

Tectaria trifoliata (L.) Cav. Moist rocky ravines in rain forest areas at chiefly middle elevations, Proctor (1977).

Tectaria incisa Cav. Base of boulders and damp banks in open forest. Route to Source, c.1600 feet, 1988 and 1990, 32,33(BM); 29(NMW.V91.115.08).

Ctenitis meridionalis (Poiret) Ching. Sheltered bank above ghut east of Tower Hill, four or five plants, 1200 feet, 1990, 482,483(BM); 484,485,486(NMW.V91.115.100). **New Record**.

Diplazium limbatum (Willd.) Proctor. Wet shaded ravines at lower to middle altitudes, Proctor (1977).

Diplazium cristatum (Desr.) Alston. Frequent along route to Source in margin of forest, c.1600 feet, 1990, 7(NMW.V91.15.01).

Diplazium striatum (L.) C. Presl. On shady bank of ravine by side of route to Source, c.1600 feet, 1990, 8(NMW.V91.115.02).

Thelypteris sancta* (L.) Ching. On rock face at Source, c.1700 feet, 1990, 123(BM); 124(NMW.V91.115.27). If identification confirmed a **New record. (Fig. 12).

Thelypteris limbata (Sw.) Proctor. Exposed slopes and low montane thickets on the summits of volcanic mountains, Proctor (1977).

Thelypteris balbisii (Sprengel) Ching. Secret garden at Golden Rock, originally from mountain, c.850 feet. 1988 and 1990, 158(NMW.V91.115.33).

Thelypteris aff. *balbisii*. Indusium dark brown, persistent, large. Sheltered site on route to Source by edge of forest, c.1600 feet, 1990.

Thelypteris aff. *balbisii*. Summit thicket by triangulation point, 3232 feet, 1990, 176(BM); 177(NMW.V91.115.37), 179(NMW.V91.115.38). (Similar to *Thelypteris limbata* (Sw.) Proctor, but lacks indusia).

Thelypteris germaniana (Fée) Proctor. Moist forested slopes at higher elevations, Proctor (1977).

Thelypteris muscicola Proctor. Summit of Nevis Peak. Very rare, endemic to Nevis, c.3220 feet, 1990, 161(BM); 163(NMW.V91.115.34).

Thelypteris decussata (L.) Proctor. Restricted to humid forest and cloud forest. Above Tower Hill, c.2000 feet, 1990, 130, 131, 132(BM). Above Zetlands in ravine, c.2200 feet, 1990. Near summit in cloud forest, c.3220 feet, 990, 139(BM); 134, 135, 136(NMW.V91.115.85), 140(NMW.V91.115.29). Fronds up to 3 metres long. **New record**. (Fig. 13).

Thelypteris clypeolutata (Desvaux) Proctor. Source, c.1600 feet, 1990, 164, 165(NMW.V91.115.35). Above Tower Hill, c.1700 feet, 1990.

Thelypteris glandulosa (Desvaux) Proctor. In deep shaded forest above route to Source, c.1600 feet, 1990, 420, 421, 422(BM); 430, 431(NMW.V91.115.89).

Thelypteris patens Sw. var. *scabriuscula* (C.Presl) A.R. Smith. Forest borders and moist, partly shaded situations along roadsides and gullies at lower to middle elevations, Proctor (1977).

Thelypteris normalis (C. Chr.) Moxley. Route to Source, 1500-1600 feet, 1990, 172(BM). Bank by Rawlins village, 1990, 174(NMW.V91.115.36). **New record**.

Thelypteris dentata (Forssk.) E. St John. Route to Source, 1200-1500 feet, 1990, 181(BM); 180(NMW.V91.115.39). **New record**.

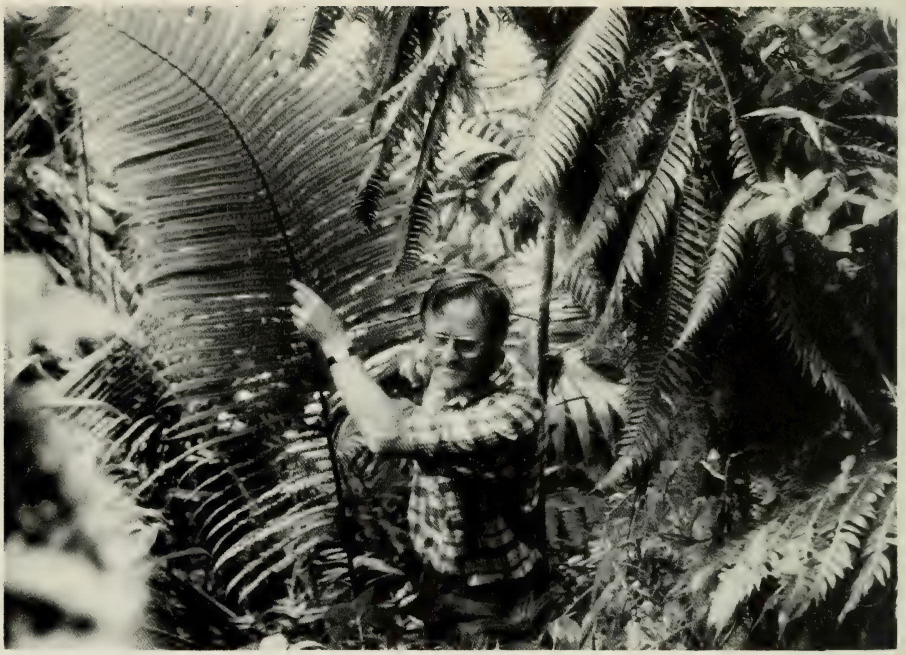

FIGURE 13. *Thelypteris decussata* in elfin forest.

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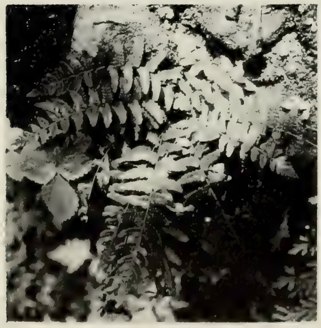

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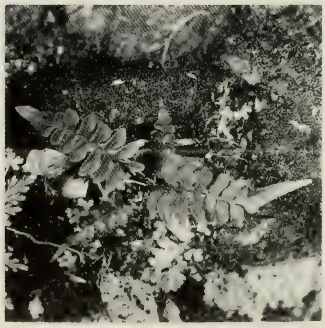

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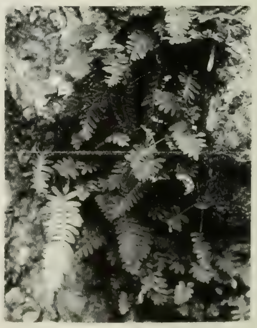

FIGURE 14. *Thelypteris reptans* var. *tenera* at Source.
FIGURE 15. *Asplenium abscissum.*
FIGURE 16. *Polypodium polypodioides* on tree in dry evergreen forest.

Thelypteris reptans (J. F. Gmelin) Morton var. *tenera* (Fée) Proctor. On rock face at Source, c.1600 feet, 1990, 126(BM); 129(NMW.V91.115.28). (Fig. 14).

Thelypteris tetragona (Sw.) Small var. *tetragona.* Base of walls in grounds of Golden Rock, c.900 feet, 1988 and 1990, 116(BM); 120(NMW.V91.115.26). Also in dry forest at around 1000 feet, 1990.

Thelypteris nephrodioides (Klotzsch) Proctor. Source, c.1600 feet, 1990, 155(NMW.V91.115.32).

Thelypteris poiteana (Bory) Proctor. Moist shaded banks, thickets and shady ravines at lower to middle elevations; plants often grow in shaded situations of cultivated areas, Proctor (1977).

Thelypteris reticulata (L.) Proctor. Along route to Source and at Source, 1500-1650 feet, 1988 and 1990, 142(BM); 143(NMW.V91.115.30); 148, 149(NMW.V91.115.31).

Asplenium laetum Sw. Ghut east of Tower Hill, c.1200 feet, 1990. Route to Source on open rock face near dripping water at head of ravine, c.1500 feet, 1990, 88(NMW.V91.115.19).

Asplenium abscissum Willd. in L. On rocks at Source, c.1600 feet, 1990, 80(NMW.V91.115.18). (Fig. 15). One collection at this site was atypical resembling *Asplenium malcolm-smithii* Proctor, 1990, 76(NMW.V91.115.17).

Asplenium auritum var. *rigidum* (Sw.) Hook. On mossy tree trunks, occasionally on boulders, at middle elevations; plants common, Proctor (1977).

Asplenium cristatum Lam. Damp cliff at Source by long ladder, c.1650 feet, 1990, 88(BM); 92(NMW.V91.115.20).

Polypodium pectinatum L. On trees above small reservoir at Source, c.1600 feet, 1990. **New record**.

Polypodium polypodioides (L.) Watt. Resurrection Fern. Walls and trees at low altitudes in light shade. Golden Rock on walls, c.850 feet, 1988 and 1990, 454(NMW.V91.115.94). Above Golden Rock in dry forest scrub on tree trunk, c.950 feet, 1990. (Fig. 16).

Polypodium loriceum L. Epiphytic at medium to high altitudes in damp forest. Above Tower Hill, 1700-2400 feet, 1990, 445(NMW.V91.115.92). Cloud forest at summit of mountain, c.3220 feet, 1990, 448(NMW..V91.115.93).

Polypodium triseriale Sw. Light forest above Tower Hill, c.1700 feet, 1990, 436,437(NMW.V91.115.90). Route to Source, 1500-1600 feet, 1990.

Polypodium aureum L. var. *aureum*. Rabbit's-foot Fern/Golden Polypody. Shady wall at low altitude by road leading up to Golden Rock, c.850 feet, 1988 and 1990, 476,477(BM); 469,470,471(NMW.V91.115.98).

Polypodium piloselloides L. Snake Polypody. On stone walls and tree trunks on route to Source, 1500-1600 feet, 1988 and 1990, 467(NMW.V91.115.97).

Polypodium lycopodioides L. Stone walls and trees. Golden Rock, c.850 feet, 1988 and 1990. Tree trunk in dry forest above Golden Rock, c.950 feet, 1990. Route to Source, 1400-1600 feet, 460(NMW.V91.115.95), 463(NMW.V91.115.96).

Polypodium phyllitidis L. Florida Strap Fern. Trees near Source, c.1600 feet, 1990, 440(NMW.V91.115.91).

Grammitis serrulata (Sw.) Sw. Source, covering rocks above water level in Source reservoir, c.1600 feet, 1988 and 1990, 311(NMW.V91.115.63). Epiphytic in moss on trees above Zetlands, c.2300 feet, 1990. Epiphytic in moss on trees above Tower Hill, c.2800 feet, 1990, 309(NMW.V91.115.62). Epiphytic in moss on trees at summit, c.3220 feet. 1990. Common.

Grammitis serricula (Fée) Proctor. On mossy trees at high elevations, Proctor (1977).

Grammitis flabelliformis (Poiret in Lamarck) Morton (*G.taenifolia* (Jenman) Proctor). Epiphytic in moss festooning trees in summit cloud forest, c.3230 feet, 1990, 320(NMW.V91.115.66).

Grammitis suspensa (L.) Proctor. Cloud forest above Tower Hill, c.2700 feet, 1990, 318(NMW.V91.115.65).

Grammitis asplenifolia (L.) Proctor. Forest above Tower Hill, c.1700 feet, 1990, 315(BM); 314(NMW.V91.115.64).

Grammitis seminuda (Willd.) Willd. (*Cochlidium seminudum* (Willd.) Maxon). Epiphytic on trees often in moss festooning trees. Above Zetland, 1600-2300 feet, 1990, 357(NMW.V91.115.77). Above Tower Hill, 2600-2800 feet, 1990.

Vittaria lineata (L.) Smith. Shoestring Fern. Above Tower Hill epiphytic on tree, c.1200 feet, 1990, 328(NMW.V91.115.69). Route to Source, 1988.

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The authors wish to thank Dr Dennis Adams of the Natural History Museum for kindly agreeing to check our determinations and correct us in several instances. They would also like to thank Robert Young, Dean Rodriques and their colleagues of Vanier College, Quebec, Quentin Henderson on Voluntary Service Overseas and Pam Barry of Golden Rock Hotel for helping us in so many ways on Nevis. Also no collecting would have been possible without the ready permission given by O. Samuel Powell, Director of Agriculture, Nevis.

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REVIEW

SPORES OF THE PTERIDOPHYTA by Alice F. Tryon and Bernard Lugardon, 648 pp., 393 figs. 1990. Springer-Verlag, Berlin. ISBN 3-540-97218-8. Price DM 188.

This book is an encyclopaedic reference work to the development and structure of pteridophyte spores. A short but comprehensive Introduction discusses new concepts on sporoderm development and ultrastructure and the relationship between spore and pollen sporoderms, clarifying and describing, often new, terminology of spore wall-layering. There is an interesting section on possible lines of evolution of different spore types. Both SEM and transmission electron micrographs are given for each genus, and the techniques used in preparation are briefly described.

The text describing the spore morphology and commenting on its diversity and relationships is arranged in a family order only remotely similar to that used in Tryon and Tryon (1982). It is not clear whether either the family or the generic arrangement is based on spore morphology although the reader can suspect it is, giving us yet another perspective on this never ending debate; 232 accepted genera are treated, arranged in 35 families. In many larger genera a range of species and micrographs are pictured, e.g. *Asplenium* (73), *Cheilanthes* (55), *Dryopteris* (50), *Isoetes* (52), *Selaginella* (87), *Sphaeropteris* (33), *Thelypteris* (35). Several British species (and specimens) are figured; Figs 38, 39 of *Isoetes echinospora* from English material look very much like the fertile hybrid *I. echinospora* × *lacustris*, yet to be cytologically confirmed for Britain.

A C JERMY

CHLOROPLAST DNA AND MORPHOLOGICAL VARIATION IN THE FERN GENUS *PLATYCERIUM* (POLYPODIACEAE: PTERIDOPHYTA)

JOHANNES M. SANDBRINK*, ROELAND C.H.J. VAN HAM and
JAN VAN BREDERODE
Department of Botanical Ecology and Evolutionary Biology
University of Utrecht, Padualaan 8, 3584 CH Utrecht,
The Netherlands

* To whom all correspondence should be addressed. Present address:
Centre for Plant Breeding and Reproductive Research, Mansholtlaan 15,
6708 PA Wageningen, The Netherlands

ABSTRACT

The phylogenetic relationships of 15 species of the pantropical staghorn fern genus *Platycerium* (Polypodiaceae) have been studied, using chloroplast DNA and morphological data. Restriction fragment length polymorphisms (RFLPs) of chloroplast DNA among eleven species of genus *Platycerium* have been examined.

The patterns of interspecific RFLPs were too complex to allow for a direct study of mutational events. Therefore, a simplified method was adopted to reveal the relatedness of the observed restriction fragment patterns: assignment of fragment homology was based upon critical inspection of the fragment patterns. This resulted in the recognition of 215 fragments shared by at least 2 species. A binary data matrix was compiled from the presence/absence distribution of these fragments over the species. Both cladistic analysis using Wagner parsimony and agglomerative clustering analysis of the data revealed the same pattern of relationships among the species. The results from the chloroplast DNA analysis were compared with the results from cladistic and agglomerative clustering analysis of a morphological dataset comprising 85 multistate characters. The results of the study lead to a new hypothesis on the phylogeny of *Platycerium*, that is highly congruent with geographic distributions.

INTRODUCTION

The tropical fern genus *Platycerium* Desv. (staghorn ferns, Polypodiaceae) comprises 15 species (Hennipman & Roos 1982) or 18 species (Joe Hoshizaki 1972), mainly distributed in the Palaeotropics, with only one species in the Neotropics. The genus unambiguously is a monophyletic group, but there has been controversy about the systematic position of the genus among other genera of polypodiaceous ferns and the infrageneric relationships (Hennipman & Roos 1982). *Platycerium* and its sister genus *Pyrrosia* Mirbel constitute one of the two subfamilies within the *Polypodiaceae*, viz. the *Platycerioideae* (Hennipman et al. 1989). Among ferns, this subfamily is characterized by the unique possession of stellate hairs. Most studies on *Platycerium* that have appeared in this century deal with its morphology and taxonomy (Straszewski 1915; Bower 1928; Joe 1964; Joe Hoshizaki 1970, 1972; De Joncheere 1974; De Joncheere & Hennipman 1970 and Hennipman & Ros 1982). The geographical distribution of the species (FIG. 1) have been studied by Hennipman and Roos (1982). The evolutionary relationships within the genus have been studied by both Joe Hoshizaki (1972) and Hennipman and Roos (1982). These authors come to very different conclusions (FIG. 2 and FIG. 3). Joe Hoshizaki (1972) recognizes eighteen species, which she assumes to represent three main lines of evolution in the genus. Her groups coincides with sympatry at a continental level: she recognizes a Javan-Australian (the middle branch in FIG. 2), an Afro-American (the left branch) and a Malayan-Asiatic group (the right branch). Within their respective geographical areas the species mostly have disjunct distributions.

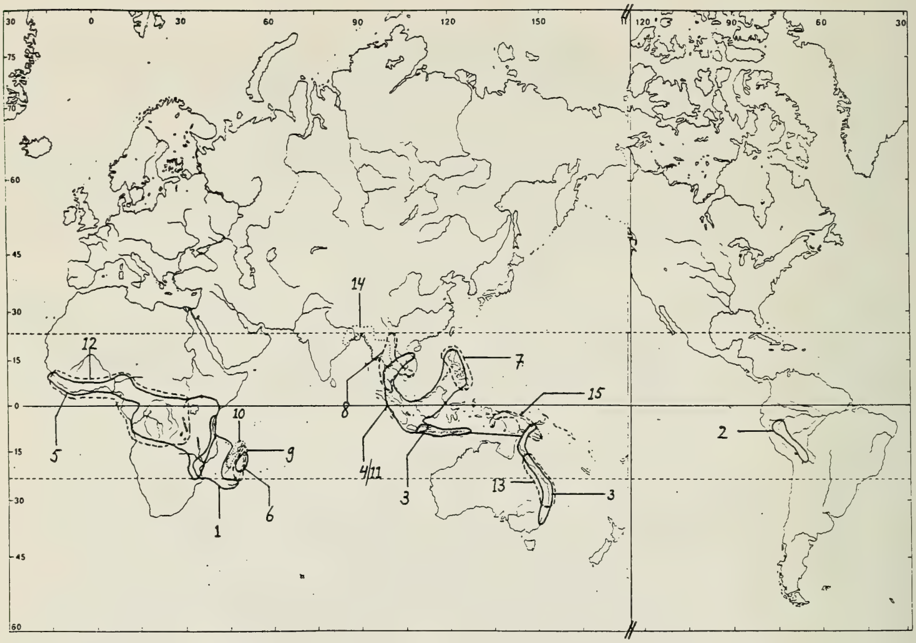

Figure 1. Global geographical distribution of *Platycerium* species descriptions by Hennipman & Roos (1982).

1.. *P. alcicorne* 2. *P. andinum* 3. *P. bifurcatum* 4. *P. coronarium* 5. *P. elephantotis* 6. *P. ellisii* 7. *P. grande* 8. *P. holttumii* 9. *P. madagascariense* 10. *P. quadridichotomum* 11. *P. ridleyi* 12. *P. stemaria* 13. *P. superbum* 14. *P. wallichii* 15. *P. wandae.*

Numbers and abbreviations assigned to the different species are the same in all figures.

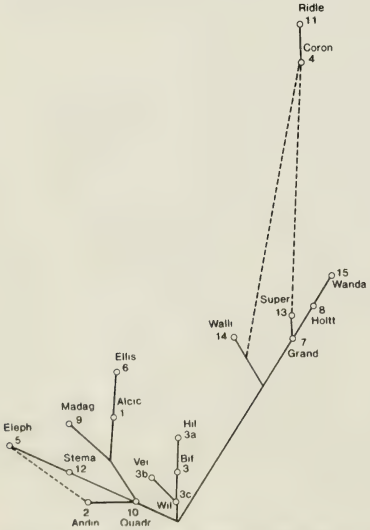

Figure 2. A modified representation of the lines of evolution of *Platycerium* species from Joe Hoshizaki (1972).

1. *P. alcicorne* (alcic), 2. *P. andinum* (andin), 3. *P. bifurcatum* ssp. *bifurcatum* var. *bifurcatum* (bif) 3a. *P. bifurcatum* ssp. *bifurcatum* var. *hillii* (hil) 3b. *P. bifurcatum* ssp. *veitchii* (vei) 3c. *P. bifurcatum* ssp. *willinckii* (wil) 4. *P. coronarium* (coron), 5. *P. elephantotis* (eleph) 6. *P. ellisii* (ellis) 7. *P. grande* (grand) 8. *P. holttumii* (holtt), 9. *P. madagascariense* (madag) 10. *P. quadridichotomum* (guadr), 11. *P. ridleyi* (ridle), 12. *P. stemaria* (stema), 13. *P. superbum* (super), 14. *P. wallichii* (walli), 15. *P wandae* (wanda).

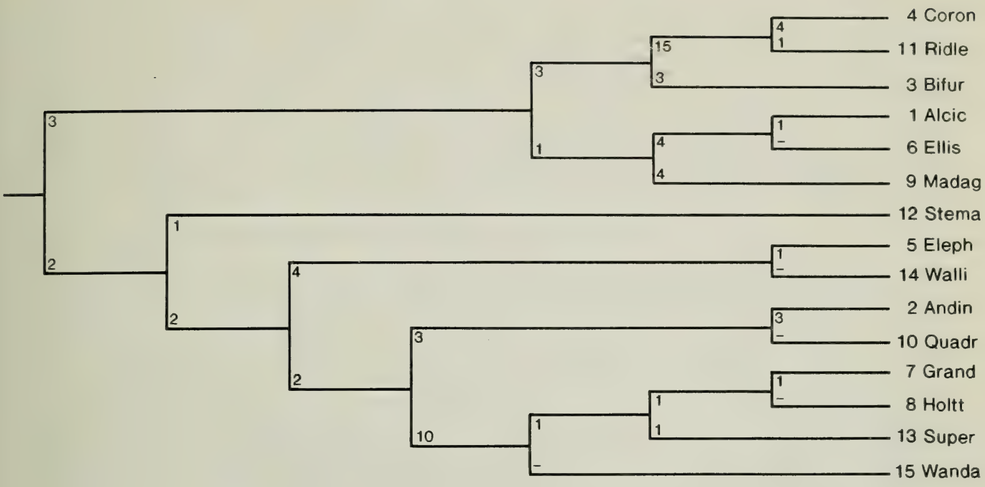

Figure 3. The phylogeny of the genus *Platycerium* according to Hennipman and Roos (1982). The number of apomorphies on which grouping is based are given in the tree.

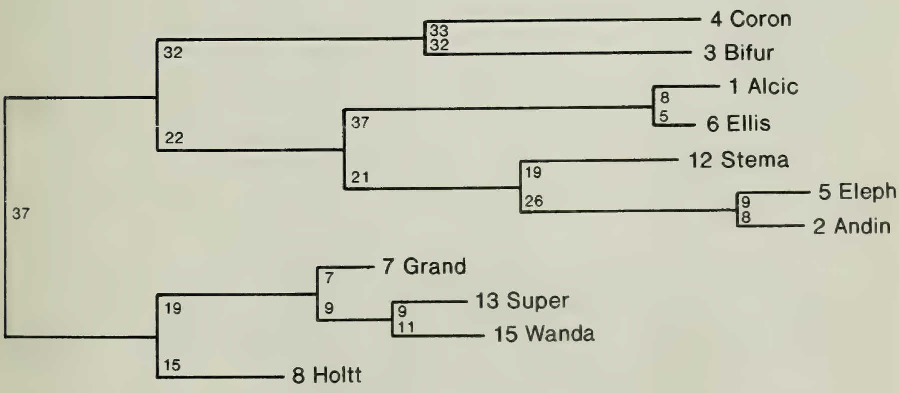

Figure 4. One of the minimal mutation trees found with the BANDB option implemented in the computer program PAUP using the molecular dataset. The next tree found had the three-taxon cluster including *P. andinum* attached to the four-taxon *P. grande*-group (see text). The number of steps or mutations in each branch are given.

Because Hennipman and Roos (1982) have reduced the specific status of four species attributed by Joe Hoshizaki (1970) to the polymorphic *P. bifurcatum*-complex, to infraspecific taxa of *P. bifurcatum* (FIG. 2, 3a-c), they recognise only 15 species. Unlike the three lines of evolution distinguished by Joe Hoshizaki, Hennipman & Roos (1982) recognise two major monophyletic groups, (consisting of lower-ranked taxa that comprise allopatric species at a continental level (FIG. 3). As an example, their *P. elephantotis*-group relates a Central African species to a South East Asian species. In biogeographic terms, this is a less parsimonious solution than Joe Hoshizaki's separation of the species into the Afro-American and Malayan-Asiatic group, respectively.

In the case of allopatric speciation, fragmentation of an ancestral species into two or more different species may result from the physical separation of a distribution area (vicariance; Wiley, 1980) or after long-distance dispersal. Under the assumption that *Platycerium* arose on one of the present-day continents, the distribution pattern of the species is most parsimoniously explained by the phylogeny of Joe Hoshizaki (1972), because it requires a smaller number of dispersal events when compared to the phylogeny of Hennipman and Roos (1982): 2 long- and 2 short- versus 4 long- and 2 short-distance dispersal events, respectively. If the origin of the genus precedes the time of continental fragmentation, then vicariance could have been involved as a mode of allopatric speciation as well as dispersal. Both phylogenies discussed above were inferred from morphological data. Hennipman and Roos (1982) based their phylogeny on a cladistic analysis of selected morphological characters, preceded by *a priori* interpretations of apomorphic and pleisiomorphic character states, using outgroup comparison. Joe Hoshizaki (1972) refers to Wagner's (1962) ground plan divergence method. However, the lack of distinct, informative morphological characters may account for the differences between previous classifications of *Platycerium*.

Comparative data of chloroplast genomes has recently become a major tool for assessing phylogenetic relationships among angiosperm plants at diverse taxonomic levels (Palmer, 1986a, 1987, Palmer et al. 1988 and references therein): the relatively high degree of overall sequence and size conservation of chloroplast DNA (cpDNA) among closely related species as well as among the major lineages of flowering plants makes it an ideal source of variation for evolutionary studies above the population level. In addition, unisexual inheritance, as the most frequent mode of chloroplast transmission in angiosperms (Whatley, 1982), can provide strong evidence for the parentage within hybrids and polyploid complexes (e.g. Palmer et al. 1983a; Stein 1985; Erickson et al. 1983; Kung et al. 1982). The chloroplast genome of ferns is less well studied than that of angiosperms. Most of the studies of fern cpDNA deal only with the characterization of the genome (Palmer & Stein 1986; Hasebe & Iwatsuki 1990). Until recently very few taxonomic studies of pteridophytes using chloroplast DNA have been published: Stein et al. (1986) on the genus *Osmunda* and Yatskievych et al. (1988) and Stein et al. (1989) on the cpDNA evolution of the genera *Cyrtomium*, *Polystichum* and *Phanerophlebia* (Dryopteridaceae).

In the present study we compare results of an analysis of cpDNA variation in the fern genus *Platycerium* with an analysis based on morphological data. Eleven species of the genus *Platycerium* were examined using restriction endonuclease analysis of their cpDNA. Although an account of the specific mutation events could not be given for the observed restriction fragment variation, relationships are inferred from comparisons of interspecific restriction fragment length polymorphisms. In addition, a morphological dataset of 85 multistate characters, including all fifteen species of the genus was compiled from the literature. Parsimony and cluster analyses were performed on both cpDNA and morphological data matrices. The results of these analyses have been compared with the previous morphological studies, and a new hypothesis on the phylogeny of the genus is presented.

MATERIALS AND METHODS

Plant material

Nineteen specimens of eleven species, representing the eight main groups in the genus as postulated by Hennipman and Roos (1982), were examined (Table 1). The remaining four species *(P. madagascariense, P. quadridichotomum, P. ridleyi* and *P. wallichii)* were either unavailable or of insufficient material.

The sources of plant material for the species of *Platycerium* included in the analysis are shown in Table 1. All investigations were carried out on full-grown specimens, which had been collected in the field and cultivated under tropical greenhouse conditions in the botanic gardens of the Universities of Utrecht and Leiden.

Table 1. Accessions of *Platycerium* included in the analysis of chloroplast DNA variation.

	Species	**Garden nr.**
a.	*P. alcicorne* Desv.	82.259
b.	*P. andinum* Baker	85.164
c.	*P. bifurcatum* (Cav.) C. Chr. s.l.	X-1
d.	ssp. *bifurcatum* var. *veitchii* (Underwood) Hennipm. & Roos	81-181
e.	ssp. *bifurcatum* var. *hillii* (T. Moore) Domin.	20684
f.	ssp. *bifurcatum* var. *hillii* (T. Moore) Domin.	20689
g.	ssp. *bifurcatum* var. *hillii* (T. Moore) Domin.	82-354
h.	*P. coronarium* (Konig ex Muller) Desv.	82-220
i.	*P. coronarium* (Konig ex Muller) Desv.	20676
j.	*P. coronarium* (Konig ex Muller) Desv.	20679
k.	*P. elephantotis* Schweinf.	82-356
l.	*P. ellisii* Baker	82-258
m.	*P. grande* (Feé) Kunze	23044
n.	*P. holttumii* De Jonch. & Hennipm.	16638
o.	*P. stemaria* (Beauv.) Desv.	82-178
p.	*P. stemaria* (Beauv.) Desv.	82-355
q.	*P. stemaria* (Beauv.) Desv.	X-2
r.	*P. superbum* De Jonch. & Hennipm.	20681
s.	*P. wandae* Racib.	180

Chloroplast DNA isolation

Chloroplast DNA (cpDNA) was isolated according to Sandbrink et al. (1989). Prior to harvesting, plants were kept in the dark for 4 to 8 days to reduce the starch content of the plastids. Leaves were ground at 4°C in a Waring blender with homogenization buffer (HB) (1.25 M NaCl, 3 % PVP, 15mM 2-ME, 0.1% BSA, 7mM EDTA, 10 mM Tris-HCl, pH=8.0). in a 1:5 (w:v) ratio. The chloroplast suspension was filtered through 1 layer of nylon gauze and 4 layers of Miracloth (Calbiochem). Chloroplasts were centrifuged at 1500 x g, resuspended in HB, centrifuged again at 1500 x g and resuspended in a buffer containing 5 mM EDTA, 10 mg/ml proteinase K and 10 mM Tris-HCl, pH=8.0 (8:1 w:v). For leaves that were somewhat aged the chloroplasts were washed twice in HB. An equal volume of lysisbuffer (10 mM 2-ME, 5 mM EDTA, 4% sarkosyl, 1% SDS, 10 mg/ml proteinase K, 10 mM Tris-HCl, pH=8.0) was added. Chloroplasts were lysed by incubation for 30 min at 37°C followed by 30 min. of gentle rotation at room temperature. The lysate was centrifuged for 10 min at 3,000 x g to remove debris and residual starch (mainly in form of amyloplasts). An equal volume of 2 x CTAB buffer (1.4 M NaCl, 20 mM 2-ME, 20 mM EDTA, 2% cetyl trimethyl ammonium bromide, 100 mM Tris-HCl, ph=8.0) was added.

The suspension was incubated for 1 h at 60°C and subsequently extracted twice with chloroform; isoamylalchohol (24:1). DNA was precipitated with isopropanol at -20°C and pelleted by centrifugation at 10,000 x g. Pellets were washed in 76% ethanol, 10 mM ammonium acetate and finally resuspended in TE Buffer pH=8.0 (Maniatis et al., 1982). Restriction endonucleases were purchased from Pharmacia and Boehringer Mannheim.

The following restriction enzymes were used: for infraspecific cpDNA variation: Bgl II, BstE II, Dra I, Hind III, Nco I, Pvu II, Sal I, Sca I, and Sma I, and for interspecific cpDNA variation: Bgl II, BstE II, Mlu I, Nco I, Pst I, Sac I, Sal I, Sca I, and Sma I. Electrophoresis was on 0.3-0.7% TBE agarose minigels (Maniatis et al., 1982).

Restriction fragment pattern analysis

The observed pattern of interspecific restriction fragment variation among the *Platycerium* species examined was too complex to allow a direct study of mutational events. Therefore a simplified method was used to reveal the relationships of the obtained restriction fragment patterns: in our approach every individual band of the digested cpDNA was treated as a discrete phenotypic character of the species in question. Fragments with the same relative migration distance were treated as homologies. The inferred homologous restriction fragments of all cpDNAs examined were compiled into a binary data matrix which was subjected to further analysis. In their study of chloroplast DNA variation in *Silene* sect. *Siphonomorpha*, Sandbrink & Van Brederode (1991) found that the patterns of restriction fragment of cpDNA were also too complex to allow for a direct study of mutational events. They showed, that the method described above resulted in the same shortest Wagner and Dollo trees as the more traditional method of identification of restriction site mutations by the hybridization-overlap method (Palmer 1986b).

Morphological variation

Characters and character state distributions were mainly taken from the species descriptions in Hennipman & Roos (1982). In addition, eight characters, representing 22 character states, were taken from Joe Hoshizaki (1972).

Data analysis

The molecular and morphological data matrices were subjected to two types of analysis: 1) agglomerative clustering analysis using the program system BIOPAT (Hogeweg and Hesper, 1972). A phenetic cluster analysis on the data matrices was performed on mean character differences, using the cluster criteria of Ward's averaging (Ward 1963) and group averaging (UPGMA: Sokal & Sneath 1963), implemented in the BIOPAT program DENDRO. 2) numerical cladistic analysis using the computer program "Phylogenetic Analysis Using Parsimony" (PAUP version 2.4.1) developed by Swofford (1985). In the cladistic analysis of the molecular data matrix the most parsimonious trees were searched for by the brand-and-bound algorithm of Hendy and Penny (1982), implemented in PAUP by the BANDB-option. For the morphological data matrix, most parsimonious trees were searched for by applying the global branch-swapping algorithm (SWAP-GLOBAL-option) with the MULPARS-option to retain all equally parsimonious trees. All characters were treated as unordered. Missing data, due to logistical or technical problems were present in the molecular data matrix. In PAUP, such data do not affect tree-construction procedures, where character states to missing characters are parsimoniously assigned only after the building-up of a tree (Swofford, 1985). Molecular and morphological data matrices with descriptions of the morphological characters and character states are presented in the Appendices 1-3.

RESULTS

Infraspecific cpDNA variation

Infraspecific variation was examined among 3 specimens of *P. coronarium* (acc. h-j), 3 specimens of *P. stemaria* (acc. o-q) and 5 specimens of *P. bifurcatum* (Table 1). One specimen of ssp. *veitchii* (accession d), three specimens of the ssp. *P. bifurcatum* variety *hillii* (acc. e-g) and one specimen of undetermined subspecific rank (acc. c), represented the *P. bifurcatum* accessions. Specimens of *P. bifurcatum* ssp. *willinckii* were not available. For the other species only one appropriate specimen was available for cpDNA analysis. Comparisons between pairs of restriction fragment patterns enabled estimation of infraspecific genetic similarity for the chloroplast genomes of *P. bifurcatum, P. coronarium* and *P. stemaria.* As an index of the relative genetic similarity, the fraction of shared restriction fragments was used according to Nei and Li (1979): $F = 2Nxy / (Nx + Ny)$ in which F is the fraction of shared restriction fragments, Nx and Ny are the numbers of fragments in species x and y, respectively and Nxy is the number of fragments shared by x and y. Table 2 shows the values of F for the pairs of specimens compared. The interspecific pairs *P. alcicorne – P. ellisii, P. alcicorne – P. andinum, P. alcicorne – P. grande* and *P. andinum – P. grande* are added for comparison.

Infraspecific variation within species of *Platycerium* as detected in this study, is considerably lower than interspecific variation. Maximal infraspecific divergence was found between the specimen of *P. bifurcatum* ssp. *veitchii* and the three specimens of *P. bifurcatum* ssp. *bifurcatum.* The least diverged species couple *P. alcicorne – P. ellisii,* according to the interspecific cpDNA and morphological variation, showed a divergence considerably higher then the scored infraspecific variation.

Table 2. Quantitative analysis of infraspecific cpDNA variation by means of proportions of shared restriction fragments (F) Specimen designations refer to garden numbers (Table 1). For explanations of symbols see text.

Species	**Specimen-couple**			Nxy	Nx +Ny	F
P. coronarium	82-220	x	20676	114	230	0.991
	82-220	x	20679	86	173	0.994
	20676	x	20679	86	174	0.989
P. bifurcatum	X-1	x	20684	121	242	1.000
	X-1	x	20689	121	242	1.000
	X-1	x	82-354	121	244	0.992
	X-1	x	81-181	96	199	0.965
	20684	x	20689	121	242	1.000
	20684	x	82-354	121	244	0.992
	20684	x	81-181	96	199	0.965
	20689	x	82-354	121	244	0.992
	20689	x	81-181	96	199	0.965
	82-354	x	81-181	96	199	0.965
P. stemaria	82-178	x	82-355	126	256	0.984
	82-178	x	X-2	92	188	0.978
	82-355	x	X-2	84	168	1.000
P. alcicorne x *P. ellisii*				124	272	0.912
P. alcicorne x *P. andinum*				89	308	0.580
P. alcicorne x *P. grande*				50	246	0.410
P. andinum x *P. grande*				50	226	0.442

Interspecific variation

A molecular data matrix was compiled from the restriction fragment patterns by treating each restriction fragment as a separate character. The interspecific comparisons of restriction fragment patterns resulted in the recognition of 215 fragments shared by at least two species. Restriction fragment data were not complete for some accessions, due to the limited amount of proper plant material. The proportions of missing data for each species in the molecular data matrix are listed in Table 3.

Table 3. Proportion of missing data in the molecular data matrix.

Species **Data (%)**		**Proportion missing**
1.	*P. alcicorne*	0.0
2.	*P. andinum*	0.0
3.	*P. bifuractum* s.1.	0.0
4.	*P. coronarium*	0.0
5.	*P. elephantotis*	62.8
6.	*P. ellisii*	21.4
7.	*P. grande*	8.8
8.	*P. holttumii*	32.6
9.	*P. stemaria*	0.0
10.	*P. superbum*	19.5
11.	*P. wandae*	19.5

Minimal mutation analysis was performed using the branch and bound algorithm, implemented in the PAUP program (version 2.4.1). Two trees were found requiring a total number of 359 steps with a consistency index (Kluge and Farris, 1969) of 0.599. The first tree is presented in FIG. 4. The second tree was the same except for the linking of the three species of the grouping including *P. andinum* directly to the four species of the *P. grande*-grouping. This second tree, however, has 51 parallel gains of fragments, whereas the first presented tree has only 40 parallel gains. The dendrograms obtained from the agglomerative cluster analysis of the molecular data matrix using different similarity measures (mean character differences, mean square distances, Euclidean distances and correlation coefficients) and 2 different cluster criteria (Ward's averaging and group averaging) were all identical. To avoid redundancy only the dendrogram obtained from group averaging on mean character differences has been given (FIG. 5). Cluster analysis of a subset of the original data matrix (comprising the fragments generated by the enzymes Nco I, Pvu II and Sal I, a total of 83 characters) also gives the same tree.

Hereafter, the pattern of relationships among the species examined for cpDNA variation as shown in the minimal mutation tree (FIG. 4) and the dendrogram of the cluster analysis (FIG. 5) will be referred to as "the molecular tree".

The following groupings present in the molecular tree are also found in the phylogenetic hypotheses of:

A: Both Joe Hoshizaki (1972) (FIG. 2) and Hennipman and Roos (1982) (FIG. 3):

1) the *P. alcicorne*-grouping, comprising the specieis *P. alcicorne* (= *P. vassei* in Joe Hoshizaki (1972)) and *P. ellisii.*

2) the *P. grande*-grouping, comprising the species *P. grande, P. superbum, P. wandae* and *P. holttumii.* Within the *P. grande*-group however, the proposed relationships in the three phylogenetic hypotheses compared differ.

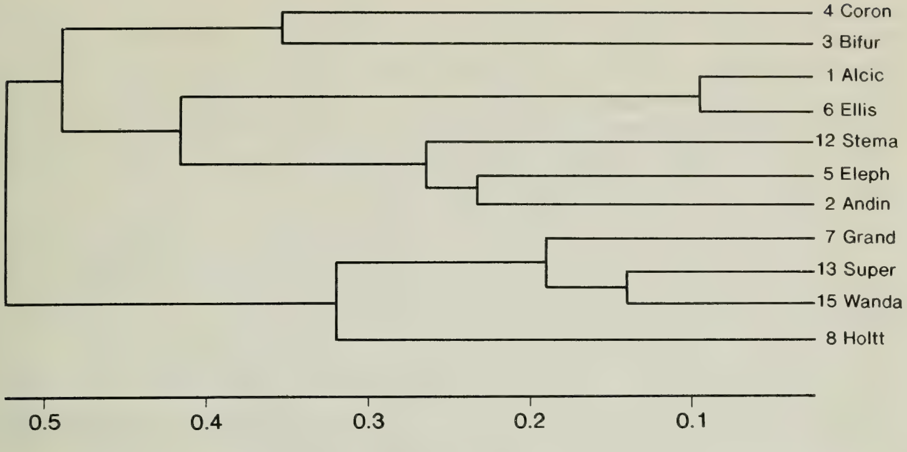

Figure 5. Representation of the clustering pattern found using the group averaging on mean character distances option of BIOPAT on the molecular dataset. The same patterns were found using other clustering criteria or similarity measures.

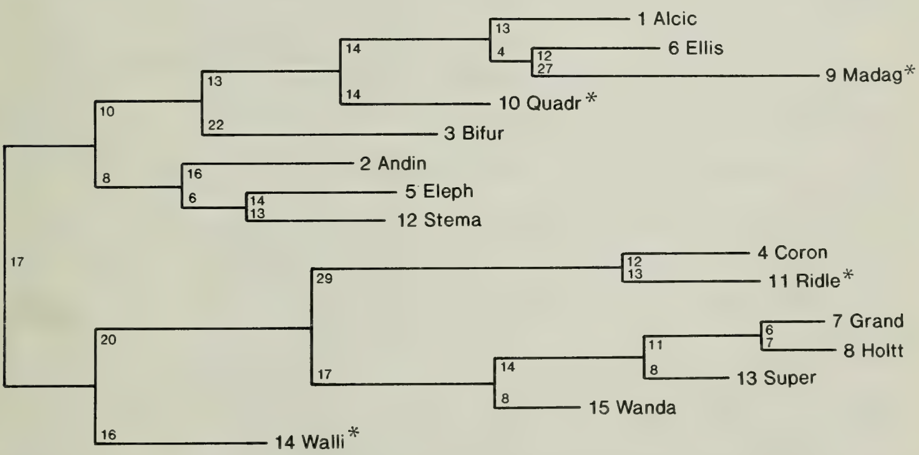

Figure 6. The minimum mutation tree found using the swap-global and mulpars options of PAUP on the morphological dataset. * indicate specifies not included in molecular analysis.

B: Joe Hoshizaki (1972)(FIG. 2):

3) the *P. andinum*-grouping, including the species *P. andinum, P. stemaria* and *P. elephantotis* (=*P. angolense).* According to Hennipman and Roos this group of species is paraphyletic.

4) the grouping of the *P. alcicorne*- combined with the *P. andinum*-grouping was found both with both cluster analysis and minimal mutation analysis. Together with the Madagascarian species *P. madagascariense* and *P. quadridichotomum* which are not presented in this cpDNA study, this grouping represents the Afro-American line of evolution within the genus as put forward by Joe Hoshizaki.

C: Hennipman and Roos (1982)(FIG. 3):

5) the *P. coronarium*-group, comprising the species *P. coronarium* and *P. bifurcatum* s.l.

Morphological variation

The morphological data matrix comprised 85 characters representing 344 character states. Character states were unordered in all parsimony analyses. In a search for minimal mutation trees with the morphological data matrix, applying the global branch-swapping algorithm of the PAUP program, yielded 2 most parsimonious trees. Both trees required a total number of 373 steps and had a consistency index (Kluge and Farris, 1969) of 0.678. The trees differed only in one branch, connecting *P. grande* either to *P. superbum* or to *P. holttumii.* The tree connecting *P. grande* to *P. holttummi* is shown in FIG. 6.

Cluster analysis on mean character differences, using group (FIG. 7) and Ward's averaging cluster criteria (not shown) was also performed on the morphological data matrix. This analysis yielded dendrograms which differed slightly from one another and from the minimal mutation trees.

P. madagascariense was monophyletic to *P. ellisii* in the minimal mutation trees and linked to the group including *P. alcicorne, P. ellisii* and *P. quadridichotomum* in the cluster analysis. *P. wallichii* was connected to the *P. grande*-group using group averaging (FIG. 7), and to the *P. andinum*-group when Ward's clustering criterion was used. Interestingly Joe Hoshizaki places *P. wallichii* near the *P. grande*-group, while Hennipman & Roos choose a closer relationship of *P. wallichii* with *P. elephantotis* in 11 species included in the chloroplast DNA study. No differences in topology were found using either clustering or with parsimony analysis (not shown).

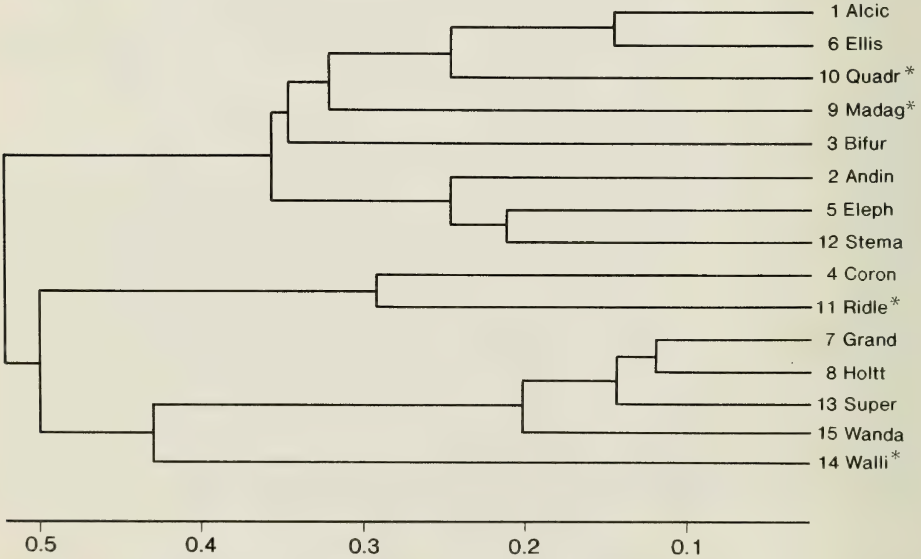

Figure 7. Representation of the clustering pattern found using the group averaging on mean character distances option of BIOPAT on the morphological data. * indicate species not included in molecular analysis.

The phylogenies found with the minimal mutation analysis of the morphological data are very similar to the phylogeny proposed by Joe Hoshizaki (FIG. 2). Corresponding groupings are:

1) the grouping comprising *P. grande, P. superbum, P. holttumii, P. wandae, P. wallichii, P. coronarium* and *P. ridleyi* (the Malayan Asiatic group of Joe Hoshizaki).

2) the grouping comprising *P. alcicorne, P. ellisii* and *P. madagascariense* (one branch in the Afro-American group);

3) the grouping comprising *P. andinum, P. stemaria* and *P. elephantotis*;
4) the grouping relating *P. quadridichotomum* to the species of grouping 2.

The first difference between the phylogenies lies in the position of *P. wallichii* relative to the *P. grande*-grouping and the *P. coronarium*-grouping; although Joe Hoshizaki does not make a decision about either the monophyly or paraphyly of the grouping comprising *P. wallichii* and the *P. coronarium*-group, it is paraphyletic in this study.

The second difference between the phylogenies lies in the position of the *P. bifurcatum*-complex relative to *P. quadridichotomum* and grouping 3: Joe Hoshizaki postulated this species combination as a separate line of evolution (the Javan Australian line), while it is here indicated to be a member of the putative Afro-American group.

There is relatively little correspondence between the cladogram of Hennipman and Roos (FIG. 3) and the morphological minimal mutation-trees. The conformity is restricted to:
1) the monophyly of the *P. grande*-, the *P. coronarium*-, and the *P. alcicorne*-group;
2) the close, though paraphyletic, relationship between *P. andinum, P. stemaria* and *P. elephantotis.*

DISCUSSION

Comparison of molecular to morphological results

When comparing the results of our analyses of the chloroplast DNA restriction fragment variation data with those of the morphological data, the following conclusions can be drawn for the genus *Platycerium*:
1) Both types of data support the presumed monophyly of three groupings of species:
a) the *P. alcicorne*-grouping, comprising the species *P. alcicorne* and *P. ellisii.*
b) the *P. andinum*-grouping, comprising the species *P. andinum, P. stemaria* and *P. elephantotis.*
c) the *P. grande* grouping, comprising the species *P. grande, P. superbum, P. holttumii* and *P. wandae.*
2) Both types of data suggest the descent of a common ancestor of the *P. alcicorne*- and the *P. andinum*-grouping, after the splitting off of the ancestor of the *P. grande*-grouping.
3) Molecular and morphological data are incongruent with regard to the relationships of the species *P. bifurcatum* and *P. coronarium*:
a) the molecular data suggest that these species are monophyletic. At the next level they are related to the united *P. alcicorne*- and *P. andinum*-grouping (FIGS. 4 & 5).
b) analysis of the morphological data suggests a sister relationship between *P. coronarium* (and *P. ridleyi* – not included in the molecular analysis) and the *P. grande*-grouping, though similarity of these taxa appears to be remote. *P. bifurcatum* then is linked to the *P. alcicorne*-grouping, but also only at a considerable level of dissimilarity (FIG. 7).

Phylogeny of the genus

In order to arrive at phylogenetic hypothesis for the genus *Platycerium* that comprises all the species, the topologies presented in this paper have been evaluated, taking into account the existing hypotheses of Joe Hoshizaki (1972) and Hennipman and Roos (1982).

The relationships proposed by the molecular tree are used as the core of this phylogeny, because these relationships are strongly supported by the invariability of the dendrograms found with various types of data analysis. Moreover, where molecular and morphological trees are incongruent the alternatives proposed by the morphological trees involve higher levels of dissimilarity or are mutually incongruent.

The phylogenetic position of the four species not included in the analysis of restriction fragment pattern variation will be discussed below:
1) *P. ridleyi:* the monophyly of the species *P. coronarium* and *P. ridleyi* is unambiguous in that the results of the analysis of morphological variation in the present study as well

as of the previous studies (Joe Hoshizaki, 1972; Hennipman and Roos, 1982) are in agreement on this point.

2) *P. quadridichotomum:* on basis of cluster analysis as well as parsimony analysis a monophyletic relationship of this species to the *P. alcicorne*-grouping is proposed. According to the phylogeny proposed by Joe Hoshizaki this species roots the two branches of the Afro-American line of evolution, thus expressing a close relationship to both the *P. alcicorne*-grouping and the species *P. andinum.* According to Hennipman and Roos *P. quadridichotomum* is monophyletic with *P. andinum* and at the next level with the *P. grande*-grouping.

3) *P. madagascariense:* minimal mutation – and cluster analysis of the morphological data suggests a monophyletic group comprising *P. madagascariense* together with the species *P. alcicorne, P. ellisii* and *P. quadridichotomum.* This monophyly is in good agreement with Joe Hoshizaki (1972) and partially with Hennipman and Roos (1982).

4) *P. wallichii:* the position of this species is not clear. It can be related either to the *P. andinum-* or the *P. grande*-grouping. The first relation is more or less in agreement with Hennipman and Roos (1982) because they propose a monophyletic relationship between *P. wallichii* and *P. elephantotis*, being a member of the *P. andinum*-grouping in the molecular phylogeny. The second relation is in agreement with Joe Hoshizaki. On the basis of the present results no further conclusions can be drawn. The aforementioned alternatives are both acceptable. Integrating the relationships of the 4 species discussed above into a phylogeny with the molecular tree as its core, the tree shown in FIG. 8 can be proposed as hypothesis on the evolutionary history of the genus *Platycerium.* Morphological and molecular four-taxon statements within the *P. grande*-grouping are not congruent. The presented phylogenetic relations within this grouping are based upon the morphological dendrograms and the ideas of Joe Hoshizaki (1972) and Hennipman and Roos (1982). Because the members of the *P. grande*-grouping had relatively high percentages of missing data in the molecular analysis (Table 3), the relationships within this group as proposed by the molecular tree may be questionable.

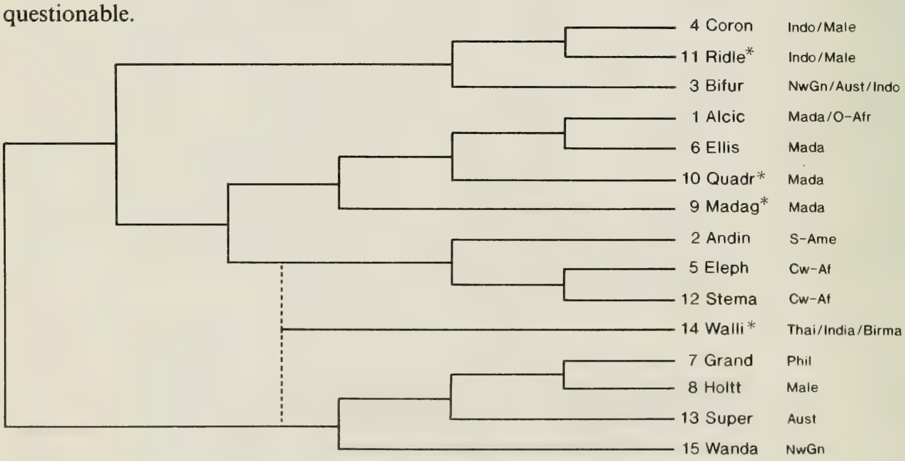

Figure 8. A tentative tree representing the ideas of the authors on the relationships within *Platycerium.* It has been constructed with the tree obtained from the cpDNA analysis as core. The morphological results (and previous phylogenies) have been used to rank the four species not included in the chloroplast DNA study and to determine final branchings in the *P. andinum* group and the *P. grande* group. Note that branch lengths do not represent any form of distance or similarity. * indicate species not included in molecular analysis.

Aust=Australia, Cw-Af=Central-West Africa, Indo=Indonesia, Mada=Madagascar, Male=Malaysia, NwGn=New Guinea, O-Afr=East-Africa, Phil=Philippines, S-Ame=South America, Thai=Thailand.

Comparison of the results with the phylogenies proposed by Joe Hoshizaki (1972) and Hennipman and Roos (1982)

The phylogenetic relationships proposed in this study are in accordance with the phylogeny of Joe Hoshizaki (1972), except for the position of *P. coronarium* and *P. ridleyi* and for details in the relationships in the Afro-American grouping. Hennipman and Roos (1982) used cladistic methods (Hennig, 1966) to elucidate phylogenetic relationships within *Platycerium*. They determined pleisiomorphous and apomorphous states of characters using outgroup comparison or in some cases, ontogeny of the character states. The results of this cladistic analysis deviated from earlier classifications and from the analysis presented in this study, although some groupings are similar. The *P. alcicorne*-grouping and the *P. grande*-grouping are present in the phylogeny of Hennipman and Roos (1982). The most remarkable group, which the phylogeny of Hennipman & Roos (1982) has in common with the phylogeny presented here, is the monophyletic group of *P. coronarium, P. ridleyi* and *P. bifurcatum*. Interestingly this group of Hennipman and Roos (1982) was based on characters where the polarity was determined using ontogenetic data. An important difference between the phylogenies of Hennipman & Roos (1982) and Joe Hoshizaki (1970) was the reduction of the specific status of four species attributed by Joe Hoshizaki (1970) to the polymorphic *P. bifurcatum*-complex (her Javan-Australian grouping), to infraspecific taxa of *P. bifurcatum*, viz. a subspecies *bifurcatum*, comprising the varieties *bifurcatum* and *hillii*, a subspecies *veitchii* and a subspecies *willinckii* (formerly *P. bifurcatum* s.s., *P. hillii, P. veitchii* and *P. willinckii*, respectively). Because the fraction of shared fragments (0.962) found within *P. bifurcatum* was significantly higher then the maximal fraction of shared fragments found on the species level (0.912 for the species couple *P. alcicorne* and *P. ellisii*), our chloroplast DNA data are in accordance with the interpretation of Hennipman and Roos (1982). However, it should be noted that *P. bifurcatum* ssp. *willinckii* has not been included in this study.

Relationships concerning the *P. andinum, P. quadridichotomum, P. stemaria* and *P. elephantotis* are totally different in the classification of Hennipman & Roos (1982). They found a sister relationship of *P. andinum* and *P. quadridichotomum* on the basis of three synapomorphic characters, all concerning the foliage fronds and soral patches. The determination of the polarity of the character states of these characters may require a re-interpretation. Parallel changes may have occurred, since these characters are very variable throughout the genus. The sister relationship of *P. stemaria* to the eight species grouping including *P. grande*, as suggested by Hennipman and Roos (1982) has been based on the shape of its base fronds only, which is also a highly variable character in *Platycerium*. The species couple *P. elephantotis* and *P. wallichii* is directly related to the six species grouping including *P. grande* and *P. andinum*, on basis of the pairwise maturing pattern of the foliage fronds only. Although this appears to be a good character, the colour of mature base fronds contradicts this grouping, but this character was omitted from their database. One of these characters must have parallel developed character states and no definite conclusions can be drawn on basis of these characters.

Phylogeny and geographical distribution

One of the interesting aspects of the presented phylogeny for the fern genus *Platycerium* is the over-all congruence of the groups with geographical distribution patterns. Splitting the tree on a four cluster level gives the following distribution:

1) A cluster including *P. alcicorne, P. ellisii, P. quadridichotomum* and *P. madagascariense* originates from Madagascar, apart from a few locations of *P. alcicorne* in East Africa.
2) A cluster including *P. andinum, P. stemaria* and *P. elephantotis* stems from America and Central Africa.
3) These two clusters are connected at the next level to an Afro-American grouping.

4) Geographic relationships within the other two clusters (the *P. grande*-grouping and the *P. coronarium*-grouping) are present although not so clear cut as those concluded in the Afro-American grouping. The *P. grande*-grouping has members in a large but fairly continuous area from Burma to Australia, and the *P. coronarium*-grouping in Australia and South-East Asia.

The results of direct comparison of restriction fragment patterns of widely diverged cpDNA lineages can not be used to calculate genetic divergences or estimate the ages of species (Sandbrink and Van Brederode, 1991). However, the low values of genetic similarity found for distantly related species in the genus (Table 2) indicate an ancient origin of *Platycerium* or an unusual high rate of mutation in chloroplast DNA in *Platycerium*. Assuming that the low genetic similarity is caused by an ancient origin, the breaking-up of the continents may have played an important role in the allopatric speciation within the pantropical genus *Platycerium*. A centre of origin in Gondwanaland was also suggested by Hennipman and Roos (1982). If vicariance has been the most important mode of speciation, sympatry at a continental level of groups of species likely supports the monophyly of such groups. A remarkable result of the analysis of chloroplast DNA variation is the support of the monophyly of the Afro-American group of species as described by Joe Hoshizaki. That the only species that occurs in South-America is related to this group can now be explained in terms of vicariance: speciation must have taken place at the time the migration of this continent away from the African continent started.

Final remarks

Further investigations of chloroplast DNA variation within the genus *Platycerium* are needed to relate the biogeographic data to its evolutionary history. Especially the inclusion of the species *P. quadridichotomum* and *P. wallichii* to the analysis is needed. No satisfying classification of *P. wallichii* could be made on basis of the outcome of the morphological data analysis. *P. wallichii* is in its present distribution restricted to the east of India, Thailand and Burma (FIG. 1), but it is the only species that occurs there. If this species would appear to be more closely related to the Afro-American *P. andinum*-group, than to the *P. grande*-grouping, it is probable that it has evolved on the Indian plate, which broke away from the African continent about 90 million years ago. Thus, vicariance via drift of the Indian plate might have been involved in speciation of the genus.

The power of chloroplast DNA variation in phylogenetic studies is greatly dependent on the taxonomic level of the group under study. This study examplifies that even in ancient or fastly evolving cpDNA lineages directly inspected restriction fragment pattern variation may reveal insight into the evolutionary history of a group of species. Because no restriction site mutation analysis could be performed, an upper limit to this approach has been reached and other techniques adjusted to the amount of divergence encountered may be used. For *Platycerium* this can be achieved by 1. choosing relatively slow evolving regions of the chloroplast genome for detailed restriction-site mapping, 2. the hybridisation overlap procedure (e.g. Jansen & Palmer, 1988) or 3. nucleotide sequencing of specific chloroplast DNA regions (e.g. the RbcL gene, Palmer et al. 1988).

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Appendix 1

The binary molecular datamatrix. Every individual band of the digested cpDNA was assigned 1. Missing data are assigned 9. Abbreviations of the taxa are as in figure 1.

```
alcic  110101011101100001001000111011001001000110010000001110001 0
0110001011001100001001010100011111000101101101001010100000101
0010100101011000110010100001010000010001100000111100110111 01
0010100000000000101001010101101011100 1
andin  11010000111100000010110010000001000110000100110101110100010 0
1100110111001000000100110001100111000001100110001000101001000
1010010000101100100001000000001100100000100101010000010100100 1
0001100011011101110011000100100110000
bifur  00101010101011110100100000000100000101110001010000001011001 0
1000011000100000000010001000010100010101000000010000110001011
0101000000001100011110100011011101011010101001110001001010 11
010000000100000010110111010101001100 10
coron  001011010011100000011000000000100001100000111000000100101 10
0101011000100000001110001000011100110101000000000000110001100
0010001000100100010000000011010000000000100101000100000010 11
0000001001000101101000100010001010110
eleph  9999999999999999999999999999999999999999999999999999999999 9
9999999999001000000100100001100111000010100100001010001000000
1010010000000100001011001100101101999999999999999999999999999
9999999999999999999999999999999999999
ellis  1101011011011000010010001110111000010001109999999999999999 9
9999999999001100001101010100011111000101101101001010100000101
0010100101011000110010100001010000000001000000001100110101 01
0010100999999999999999999999910111100 01
grand  010100000101000010100110000100010100100001110000000000110 0
0100010101011011011010100000100100101001000000001000001010000
1000000001110010010010000110100001100100010001100010010010 10
1000011999999990999999999999000101100 0
holtt  001000000101000010100110000100010000100001999999999999999 9
9999999999010011111011000001000000000000001001000110001101001
0010000011010001010011000000000000999999999999999999999999999
9999999000110010000000000000999999999
stema  110100001101000000001100100101010100010010010010011011001 00
1011010011001000011011000000100111000000010001000000100011010 00
1010000100011000000000100001010010000000001010100010101011000
1001100000000100110101010010100011001 0
super  999999999999999999999999999999999999999999999999110011001000100 1
0100010100010001111010000000000010010101100000000100000101000 0
1010001010100010010011000110000000100100010011100010010010 10
1000011110100000000010001000000000110 0
wanda  999999999999999999999999999999999999999999999999110010001000100 1
0100110100010001010010000000010000000101101001001000001000000
1010001001100000001000100011010000110010001001110001001001010
10000111101000100001100100000010001000
```

Appendix 2

Character state distributions used in the morphological analysis. Character states were mainly taken from the species descriptions in Hennipman & Roos (1982). Descriptions of the characters are given in appendix 3. Abbreviations of the taxa are as in figure 1.

Alcic	21322	11232	41121	22232	12331
31034	11122	01200	02111	11121	13111
22111	13112	32212	12132	22532	14133
Andin	21226	11112	52200	00233	22341
21032	11211	11111	12112	22122	11211
25112	22114	33545	12322	22672	13242
Bifur	21324	11332	33121	12223	12131
11035	11344	31120	02111	15321	12211
24115	82617	35344	12365	22892	15255
Coron	22141	42111	63112	31121	12132
11011	31233	51111	12121	14211	20212
26123	54421	21751	31687	11161	26446
Eleph	21226	11122	52121	12232	22321
31012	11211	01111	12122	12122	11220
22223	31214	13544	12443	22362	11062
Ellis	21212	11212	21121	12231	12131
31034	11122	01200	02111	11121	13331
22111	41114	32121	12122	22712	15312
Grand	12142	21132	12200	00113	21244
21011	22415	42112	22112	23311	20112
13123	61116	25357	22322	22222	15234
Holtt	12132	21132	32200	00113	21234
21011	22415	42112	22112	23311	20212
15123	61116	25657	22552	22542	14532
Madag	21214	11212	23200	00231	12114
32224	11122	03112	31201	11121	11111
21131	73116	12132	12354	22332	12232
Quadr	21212	11242	21121	12232	12144
31032	11211	01200	02112	22122	11211
21112	22112	14213	12111	22392	11242
Ridle	12121	52111	62112	42121	12122
12114	11122	01200	01201	11211	20212
22123	54424	41251	31776	11481	25416
Stema	21223	11132	22121	12232	22323
21032	11211	01111	12112	14122	11111
24114	41313	13444	12222	22742	15222
Super	12142	32132	11200	00113	21223
21011	22415	22112	22113	23311	20112
16123	61115	25456	22787	22752	16211
Walli	12125	11132	42121	12300	00005
01033	11216	41111	12112	12311	11212
12223	61516	33847	12622	22492	11263
Wanda	12143	32112	31121	12113	23222
21011	22415	42112	42112	23311	20212
16123	61116	24434	22111	22762	23233

Appendix 3
List of characters and character states

Social behaviour

1. Growth form	
solitary	1
in clusters	2

2. ability to reproduce from buds on roots	
present	1
absent	2

Rhizome

3. stele-type	
dictyostele	1
polycyclic-dictyostele	2
both	3

Rhizome scales

4. Length	
10 mm	1
17 mm	2
17 mm	3
10 mm	4

5. Index	
5	1
10	2
5-15	3
15	4
10	5
5	6

6. Width	
2.0 mm	1
2.0-4.5 mm	2
4.5 mm	3
4.5 mm	4
2.0 mm	5

7. Widest	
near the base	1
near the middle	2

8. Base	
truncate	1
truncate, but also rounded	2
truncate, but also cordate	3

9. Margin	
(slightly) convex	1
straight	2
both convex and straight forms	3
concave	4

10. Flabelloid margin	
present	1
absent	2

11. Apex	
acute	1
acuminate	2
both acute and acuminate	3
filiform	4
both acuminate and filiform	5
rounded	6

12. Texture	
thin coriaceous	1
(thin) papery	2
papery to thin coriaceous	3

13. Midrib	
present	1
absent	2

14. Division in midrib	
present	1
absent	2
no midrib	0

15. Shape midrib	
linear or/to narrow triangular	1
broad triangular	2
no midrib	0

16. Midrib in cross-section	
rounded	1
elliptic, rounded	2
dumpbell-shaped	3
flattened	4
no midrib	0

17. Lateral ridges	
present	1
absent	2
no midrib	0

18. Hairs	
(very) densely set	1
sparsely set	2
absent	3

19. Placement of hairs	
in narrow marginal zone	1
marginally	2
marginally and abaxially	3
no hairs	0

20. Length of hairs	
25-150 µm	1
25-250 µm	2
25 µm	3
no hairs	0

21. Branches on hairs	
present	1
absent	2
no hairs	0

22. Protuberances on hairs	
present	1
absent	2
both forms present	3
no hairs	0

23. Apical cell of hairs	
glandular	1
non-glandular	2
both types present	3
no hairs	0

24. Length of apical cell	
30 µm	1
30-60 µm	2
60 µm	3
30 µm	4
no hairs	0

25. Presence of trichomes on hairs	
always (present)	1
commonly	2
occasionally	3
rarely	4
absent	5

26. Apical cell of trichomes	
glandular	1
non-glandular	2
both types present	3
no trichomes	0

Base fronds

27. Attachment	
sessile	1
stalked	2

28. Stalk	
conspicuous	1
inconspicuous	2
not stalked	0

29. Colour of mature fronds	
green	1
green, darkening	2
withering	3

30. Position of old fronds	
recurving	1
erect	2
both recurving and erect forms present	3
appressed	4
both erect and appressed forms present	5

31. Length	
80 cm	1
80 cm	2
forms both longer and shorter than 80 cm	3

32. Width	
60 cm	1
60 cm	2

33. Position upper frond part	
appressed	1
erect	2
both appressed and erect forms present	3
spreading	4

34. Shape upper frond part	
wedge-like	1
kidney-like	2
elliptical	3
both kidney-like and elliptical forms pres.	4

35. Incisions	
with 2 main lobes	1
slightly lobed	2
strongly lobed, many dissimilar lobes	3
slightly lobed, many dissimilar lobes	4
many similar lobes	5
many ascending lobes of varying shape	6

36. Number of forkings	
1,2	1
3,4	2
1-4	3
3-6	4
1-6	5
no forkings	0

37. Margin lower part	
entire	1
sinuate	2
minutely dentate	3

38. Fringe	
present	1
absent	2

39. Exhibition of fringe	
conspicuous	1
inconspicuous	2
no fringe	0

40. Position of fringe	
above the stipe only	1
encircling the stipe	2
no fringe	0

41. Margin	
entire	1
sinuate	2
minutely dentate	3
with aphlebia like structures	4
no fringe	0

42. Veins	
prominent	1
immersed	2

43. Water storage tissue	
present	1
absent	2

44. Cells of water storage tissue	
spherical	1
cilindrical	2
no water storage tissue	0

Foliage fronds

45. Maturing of fronds	
simultaneously, in undetermined number	1
simultaneously, in pairs	2
single	3

46. Development of fertile and sterile parts	
simultaneous	1
in succession	2

47. Position	
erect	1
pendulous	2
spreading	3
both pendulous and spreading	4
all forms present	5

48. Central meristeles of stipe	
present, well developed	1
present, poorly developed	2
absent	3

49. Ring of dark fiber like cells	
present	1
absent	2

50. Number of stomata lower epidermis	
14-50/mm2	1
78-88/mm2	2

51. Palisade parenchyma	
present	1
absent	2

52. Distinctness of palisade parenchyma	
distinct	1
gradual integration into spongy mesophyll	2
poorly defined	3

53. Symmetry	
symmetrical	1
asymmetrical	2
both forms present	3

54. Forkings	
present	1
absent	2
both forms present	3

55. Transition from first to second order forkings	
gradual	1
abrupt	2
no transition	0

56. Lateral appendages	
present	1
absent	2

57. Length (cm)	
only forms 40 present	1
forms 40 and between 40-80 present	2
between 40-120	3
120	4
80	5
40	6

58. Texture	
pergamentaceous	1
leathery	2

Soral patches

59. Dependence relation between numbers of forkings and soral patches	
present	1
absent	2

60. Placement	
away from the plant	1
facing the plant	2
horizontally	3
both horizontally and facing the plant	4
all forms present	5

61. Position	
on ultimate segments and often around ultimate sinus	1
in sub-apical zone	2
apical part	3
both state 1 and 3 possible	4
specialized lobe	5
in main sinus	6
on (pen-)ultimate segments, usually reaching below first sinus	7
both state 3 and 7	8

62. Shape of soral patches	
wedge-like	1
linear or elongate	2
both wedge-like and linear forms present	3
spoon- or kidney-like	4

Sporangia

63. Sporangial development

graduate	1
mixed	2
mixed, weakly	3
mixed, strongly	4
simple	5
gradate, weakly	6

64. Shape of stalk

(2-)3-seriate	1
1-seriate	2

65. Length (µm)

260	1
300	2
300-340	3
300-340	3
260-340	4
340	5
300	6
all forms present	7

66. Index

1.3	1
1.3-1.8	2
1.8	3
1.8	4

67. Number of indurated cells

13	1
13-16	2
17-20	3
13-20	4
17	5

68. Number of epistomium cells

4	1
4	2
4 or 4	3
4 or 5	4
4, 4 or 5	5
4-6	6
5	7
4	8

69. Number of hypostomium cells

1	1
1 or 2	2
3	3
2 or 3	4
3 or more	5

70. Number of annulus cells

22	1
22-25	2
25	3
26-29	4
22-29	5
29	6
26	7

71. Length of stalk (µm)

0.3	1
0.5	2
0.5	3

72. Number of spores

8	1
64	2

73. Length (µm)

60-70	1
70-80	2
60-80	3
70-90	4
60-90	5
80-100	6
90	7

74. Width (µm)

30-40	1
40-50	2
30-50	3
50-60	4
40-60	5
30-60	6
60	7
50	8

75. Height (µm)

30-40	1
40-50	2
50-60	3
40-60	4
30-60	5
60	6
50	7

76. Periscope

distinct	1
indistinct	2

77. Dehiscence of sporangia and paraphyses

present	1
absent	2

Indument

78. Stellate hairs, number of rays

7,8	1
9,10	2
7-10	3
1-10	4
10	5
8	6
6	7
all numbers present	8

79. Length (µm)

150	1
150-250	2
250	3

250-350	4
350	5
250-450	6
150-450	7
350	8
450	9

80. Paraphyses, stalk

long	1
short	2

81. Insertion of rays

terminally only	1
terminally and sub-terminally	2

82. Number of rays

11	1
11-13	2
13	3
11-16	4
16	5
11	6

83. Shape

flat or convex	1
involute to canaliculate	2
state 1 or 2	3
short clavate	4
spine-like	5
no shape as above	0

84. Length (µm)

150	1
150-250	2
250	3
150-350	4
450	5
250	6

85. Width (µm)

30	1
30-50	2
50	3
30.70	4
70	5
50	6

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PTERIDOPHYTES OF THE STATE OF VERACRUZ, MEXICO: NEW RECORDS

MÓNICA PALACIOS-RIOS
Instituto de Ecologia, A.C. Apartado Postal 63, Xalapa,
Veracruz 91000 México

ABSTRACT

The following Pteridophyte species are reported for the first time for the state of Veracruz, México: *Adiantum capillus-veneris, Asplenium heterochroum, Ceratopteris pteridoides, Ctenitis sloanei, Diplazium induratum, Elaphoglossum monicae, Elaphoglossum revolutum, Huperzia cuernavacensis, Nephrolepis falcata* f. *furcans, Phlebodium araneosum, Polypodium hispidulum, Polypodium polypodioides var. michauxianum, Polypodium subpetiolatum, Selgainella estrellensis, Thelypteris (Goniopteris) ghiesbreghtii,* and *Trichomanes bucinatum.*

INTRODUCTION

During the last phase of research for the preparation of the Annotated Checklist of the Pteridophytes of Veracruz, México (Palacios-Rios, 1992a 1992b), I found 16 species that had not been reported, for this state. I consider them new records for Veracruz because they have not been mentioned in previous accounts, i.e., Conzatti, 1981, Fée, 1857; Finck, 1875, 1877, 1895; Fournier, 1869; Liebmann, 1848; Martens & Galeotti, 1842; Mickel & Beitel, 1988; Palacios-Rios, 1987, 1990; Rovirosa, 1909; Smith, 1981.

RESULTS

For each of the 16 species, I will present data from the voucher specimens examined (i.e., collecting site, data, collector, herbarium), its known distribution in México, and a brief description, when needed, to differentiate between closely related species.

Adiantum capillus-veneris L. Orizaba, Herbarium University of Chicago 354798, collector unknown (F); *M. Váquez et al. 379* (NY, XAL). Tropical rain forest, tropical dry forest, inhabiting gorges along streams, elevation 150-1300 m; terrestrial or epipetric herb. Local name "culantrillo", with ornamental and medicinal uses. It is easy to differentiate from related species by the presence of veins ending in teeth, with its strongly denticulate margins, with blades gradually reduced to the apex. This species has a wide distribution in México and had been mentioned as of possible occurrence in Veracruz by Palacios-Rios & Riba (1983); this is the first report based on herbarium specimens.

Asplenium heterochroum Kunze, Sumidero, *Copeland 67* (BM); temperate montane forest, on limestone, in coffee plantations; elevation 1100 m; terrestrial to epipetric herb. Closely related to *A. palmeri*, differing from that species in the nonflagelliform apex and lack of a terminal bud, thinner leaf texture, and segments more noticeably incised (Smith, 1981). This species was previously known for the state of Chiapas.

Ceratopteris pteridoides (Hook.) Hieron., Mpio. Pajapan, swamp near Barrillas, *Lot 1625* (MEXU); Mpio. Alvarado, Laguana en el Rancho "El Ensueño", ca. 5 km después de la caseta Puente Alvarado, carretera Alvarado-Tlacotalpan, *Palcios-Rios et al. 3232* (XAL); in swamps and road-side ponds; aquatic herb; sea level. This species has 32 spores per sporangium, basal pinnae of sterile frond opposite, stipe width 1-19 mm and sterile fronds mostly simple (palmately or pinnately lobed), sometimes pinnate. This species was previously known for the state of Tabasco (Cowan, 1983).

Ctenitis sloanel (Poeppig ex Sprengel) Morton, Mpio, Córdoba, Vallée de Córdoba, *Bourgeau 1838* (K, NY, UC); Mpio, Córdoba, Córdoba, *Orcutt 3214* (K, MO); elevation 1000 m; terrestrial herb. Closely related to *C. equestris* but differing in the scales of axils of pinnae which are tan to light reddish brown, rhizome and stipe base scales filiform, orangish (Smith, 1981). This species was previously known for the state of Chiapas.

Diplazium induratum Diels, Huatusco, 3 km al SE por la carretera para Fortin, *Calzada 7969* (XAL); near 8 km S of Misantla, *Conant 733 et al.* (GH, MEXU); Orizaba, Cuautlancillo, *Copeland 45* (MEXU, UC); Córdoba, *Finck 26* (MEXU); Rancho El Durazno adelante de Chocamán, cerca del Puente sobre el Río Jamapa, *Herrera et al. JB-1225* (MEXU); Córdoba, *Hutchinson (Finck 453)* (UC); Huatusco, *F. Ventura 16740* (ENCB); temperate montane forest, oak forest, inhabiting gorges along streams; elevation 750-1500 m; terrestrial herb. This species has lamina glabrous beneath; costae and rachis with scattered, lax, catenate hairs (0.8-1.0 mm long) and fibrillose scales (0.5-1.5 mm) at axils of segment midribs and costae; it is closely related to *D. lindbergii* (Mettenius) Christ of Brazil, which has smaller indusia and smaller blade scales (Mickel & Beitel, 1988). This species was previously known from the states of Guerrero, Puebla, Oaxaca, and Chiapas.

Elaphoglossum monicae Mickel, Mpio. Vigas de Ramiírez, Pedregal Las Vigas, *Bohs et al. 1757, 1775* (XAL); Mpio. Xico, Ranchería Paso Panal, camino para Positos [Pocitos], *Calzada 5740* (XAL); Mpio. Vigas de Ramírez, Volcancillo Ver. 3 km SW de Las Vigas *B. Dorantes 566* (XAL); Mpio. Vigas de Ramírez, El Volcancillo, *Dorantes 5111* (XAL); Mpio. Vigas de Ramírez, Pedregal Las Vigas, carretera Xalapa-Perote, *Dorantes & M. Acosta 2390* (XALU); Mpio. Vigas de Ramírez, El Volcancillo, *R. Ortega 530* (XAL, XALU); Mpio, Vigsa de Ramírez, Pedregal Las Vigas, *Palacios-Rios 3414* (XAL); pine forest, pine-oak forest; elevation 2200-2350(2925) m; epiphytic herb. This species was recently described for the Flora of Nueva Galicia (Mickel, 1992), and it is closely related to *E. lindenii*, differing by the oblong blade and the larger (37-49 µm) ave. 43 µm echinate-reticulate spores.

Elaphoglossum revolutum (Liebm.) Moore, Mpio. Hidalgotitlán, a 1500 m del Campamento Hermanos Cedillo hacia La Laguna, *Valdivia 942* (XAL); tropical rain forest; elevation 156 m; epiphytic herb. It is distinguished from *E. squamipes* by the generally more elliptic blade and the much lower elevations. This species was previously known for the states of Chiapas and Oaxaca.

Huperzia cuernavacensis (Underw. & Lloyd) Jolub, Las Minas. *C. Durán 925* (XAL); temperate montane forest; elevation 1700 m; epiphytic herb. This species is very closely allied to *L. taxifolium*, its leaves generally strong coriaceous and tightly appressed and occurring at higher elevations, whereas *L. taxifolium* appears to be quite variable in its leaf texture and degree of appression (Mickel & Beitel, 1988). This species was previously known only for the states of Sinaloa, Michoacán, México, Morelos, Oaxaca, and Chiapas in México.

Nephrolepis falcata f. furcans (Moore) Proctor, Nautla, *Ortega-Torres 427* (XAL). tropical deciduous forest; elevation 50 m; terrestrial herb. This cultivated species had not been previously reported for Veracruz.

Phlebodium araneosum (Martens & Galeotti) Mickel & Beitel, Mpio. Maltrata, Cumbres de Maltrata, *R. Hernández M. & C. Orozco 1645* (MEXU, MO); oak forest; elevation 1700 m; terrestrial or epipetric herb. Closely related to *Phlebodium areolatum* (Humb. & Bonpl. ex Willd.) J. Smith (=*Phlebodium pseudoaureum* (Cav.) Lellinger), but the former often has falcate pinnae, but this is not constant, blade with linear, twisted, toothed, orange scales on the lower surface, blade margin with low teeth consistently, pinnae are wider

(16-30 mm wide), rhizome scales shorter (4-7 mm), entire with a long tip. This species was previously known only for the states of Jalisco, Michoacán, Guerrero, México, Distrito Federal, Morelos, San Luis Potosí, Hidalgo, Puebla, and Oaxaca.

Polypodium hispidulum Bartlett, Soteapan, *Riba 1148a* (UAMIZ); Soteapan, *F. Ramírez 514* (XAL); tropical rain forest, *Bursera* forest; elevation 300-600 m; epiphytic herb. Related to *P. fuscopetiolatum,* but stipe and rachis stramineous below; rhizome scales ovate, acute at tip, more or less entire, blade hairy, sporangia setose (0.1-0.3 mm) and occurs at low elevations. This species was previously known for the states of Oaxaca and Chiapas.

Polypodium polypodioides var. michauxianum Weatherby, Mpio. Pueblo Viejo, vicinity of Pueblo Veijo, 2 km south of Tampico, *Palmer 542* (K, MO, US); matorral; sea level; epiphytic herb. The variety *michauxianum* has scales of lower laminar surface lacking long, acicular tip, and the upper laminar surface is glabrous. This species was previously known for the states of Coahuila, San Luis Potosí, Tamaulipas, and Chiapas.

Polypodium subpetiolatum Hook., Mpio. Orizaba, Orizaba, *Pringle 5953* (MO); Mpio. Teocelo, La Barranca, *F Ventura 15797* (ENCB, MO); temperate montane forest, oak forest, inhabiting gorges along streams; elevation 1000 m; epiphytic herb. This species resembles *P. adelphum* in the serrulate blade margin, hairy blade, and sporangia lacking long setae, but is distinct from that species in its glabrous rhizome scales, entirely free veins, and densely hairy adaxial pinnae midvein. This species was previously known for the states of Chihuahua, Sinaloa, Jalisco, Colima, Michoacán, Guerrero, México, Distrito Federal, Morelos, San Luis Potosí, Hidalgo, Puebla, and Oaxaca.

Selaginella estrellensis Hieron., Jilotepec, Xico, *Nee & Taylor 26253* (F, NY, XAL); *R. Ortega et al. 244* (NY, XAL); *C. Munoz 29* (NY); temperate montane forest, *Liquidambar-Alnus* forest; elevation 1300-1600 m; creeping herb. This species had been collected in México but the specimens were mistaken for other species of *Selaginella.*

Thelypteris (Goniopteris) ghiesbreghtii (Hook.) Morton, Hidalgotitlán, *M. Vázquez et al. 874* (XAL); tropical rain forest (jimbal); elevation 150 m; terrestrial herb. This is one of a few species of subgenus *Goniopteris* that apparently lacks stellate or forked haris. However, on the basis of other characters and its obvious affinities with *T. poiteana,* it is clearly a member of the subgenus (Smith, 1981). This species was previously known for the states of Oaxaca, Chiapas, and Tabasco.

Trichomanes bucinatum Mickel & Beitel, Xalapa; *Pringle 10809* (XAL); temperate montane forest; elevation 1200 m; epiphytic to epipetric herb. Closely related to *T. reptans,* but the former has fronds linear with shallow lobes bearing a mixture of short and long segments, the longer segments mostly near the apex; sori strongly exserted (stalks 0.5-1.0 mm long) with wide lips (1.0 mm long); margin with both forked and multi-rayed hairs, many near pinna tips Mickel & Beitel, 1988). This species was previously known only for the states of Hidalgo and Oaxaca.

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SHORTER NOTE

CHROMOSOME COUNTS FOR TWO SPECIES OF *GLEICHENIA* SUBGENUS *MERTENSIA* FROM ECUADOR

Cytological fixations were made in the field by Benjamin Øllgaard during the course of fieldwork undertaken in April 1973 for the Flora of Ecuador project by members of the Botanical Institute, Aarhus University, Denmark. He generously gave me these fixations from which I have obtained meiotic chromosome counts for two species. Herbarium vouchers are held at AAU.

1. *G. bifida* (Willd.) Spreng. Colleted by L. Holm–Nielsen, J. Jeppesen, B. Løjtnant and B. Øllgaard, number 2902 from the Province of Cotopaxi. Here it formed an extensive colony on a slope by the side of the Quevedo – Latacunga road, 46 km from Quevedo on NE exposed slopes with rain forest at 600 m altitude.

This proved to be diploid with n = 34 as have other members of this species from several areas in the New World (see Walker 1990).

2. *G. revoluta* H.B.K. Coll. no. 3614 from the Province of Zamora – Chinchipe where it grew on a slope along the road from Loja to Zamora at 17 km and at an altitude of 2400 m. The roadsides and slopes were covered by montane forest.

This plant was tetraploid with n = 68 and is a new specific record.

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TREVOR G. WALKER

Department of Biological and Nutritional Sciences, The University, Newcastle upon Tyne NE1 7RU, U.K.

REVIEW

FLORA MALESIANA, Ser. II (Pteriodophyta) Vol. 2 (1): Tectaria Group by R.E. Holttum, 132 pp. 1991. Leiden University, ISBN 90-71236-11-0. Price Dfl. 50–.

This is Eric Holttum's last major work, submitted to the editor shortly before Holttum died aged 95. It says something of this remarkable man that this substantial account maintains the very high standard that Holttum had set many years before for this Pteridophyte series of *Flora Malesiana.* The accompanying line drawings are by Peter Edwards and SEM pictures of spores of selected species give some idea of the variation seen.

Eleven genera are described: *Aenigmopteris* (5 spp.), *Chlamydogramme* (2 spp.), *Ctenitis* (28 spp.), *Cyclopeltis* (5 spp.), *Heterogonium* (17 spp,), *Lastreopsis* (4 spp.), *Pleocnemia* (17 spp.), *Psomiocarpa* (1 sp.), *Pteridrys* (6 spp.), *Tectaria* (105 spp.) *Tectaridium* (1 sp). The first two genera above are named by Holttum as a result of this revision. One hybrid in *Pleocnemia* is included, and I noted one new combination (*Pleocnemia dahlii* (Hieron). Holttum which could slip by as it was not highlighted in bold type in the index.

A C JERMY

REVIEW

THE PTERIDOPHYTES OF FRANCE AND THEIR AFFINITIES: SYSTEMATICS, CHOROLOGY, BIOLOGY, ECOLOGY. Bulletin de la Société Botanique de France vol. 138. Actualités botaniques (2) 103-237. Edited by S. Muller and M. Boudrie. 140 Ff.

This publication came from a conference in Paris on November 9th 1990 which was organised to bring together amateur and professional botanists. It was the first conference to be held in France entirely on French pteridophytes. The papers in the volume follow the different themes of the conference and given an insight into the range of work currently underway in France.

Some explore the geographical ranges of pteridophytes and discuss conservation needs. Parent describes how the Atlas of pteridophytes in Lorraine and the Vosges Mountains is progressing. Then, in another paper, he shows how the distribution of three species of *Equisetum* can be used as markers for the underlying rock strata. Lazare and Vivant, with the collaboration of Sastre, present an interesting synthesis of current knowledge and conservation status of the more than 300 taxa of pteridophytes in Guadeloupe and its dependencies. Botineau, Boudrie, Prelli and Vilks outline the official protective measures for pteridophytes in the "centre-ouest" part of France, while Muller shows that *Botrychium matricarifolium* is under threat in the Vosges Mountains due to changing patterns of land use and how appropriate land management could ensure the survival of the species.

There are papers on hybrids. Prelli uses *Asplenium* to discuss hybridization in ferns, while Bennert, Boudrie and Rasbach report on the cytology of *Asplenium* x *sarneiense* and confirm the autotetraploidy of *Asplenium billotii.* Boudrie discusses three apogamous *Dryopteris* found in France and a focusses on problem shared by pteridologists in Britain: the recognition of the sub-species of *Dryopteris affinis.* Hopefully the discussion and the table of characters will lead to a greater understanding of their distribution in France.

Other papers concentrate more on the overall morphology or developmental biology of a species. Loiseau and Felzines discuss the pioneering habit of *Equisetum* x *moorei* in the Loire valley and relate this to the mode of growth of its underground rhizome. Vindt-Balguerie outlines the development of young plants of *Huperzia selago* from bulbils. Bordonneau and Tourte discuss the embryonic development of heterosporous ferns. Then Le Coq, Guervin, Laroche and Robert briefly outline the mode of excretion of silica in *Selaginella kraussiana* and *Equisetum maximum.*

There are in addition two papers on RNA in the gametes of *Phyllitis scolopendrium* by Bajon, Blaize, Robert and Roland and in *Marsilea vestita* by Kuligowski, Ferrand and Chenou. Also a paper by Carnat, Lamaison and Boudrie on the use of thin layer chromatography in studying *Equisetum* hybrids.

Overall the papers are a good mix and contain some very useful and readable material. It is to be hoped that it will stimulate further interest in pteridophytes in France and indeed throughout Europe.

B.A. THOMAS

THE FERN GAZETTE

NOTES FOR CONTRIBUTIONS

Manuscripts on any aspect of pteridology are welcome and should be sent to:

The Editor of The Fern Gazette
Dr. Barry A. Thomas
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National Museum of Wales
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VOLUME 14 PART 3 **1992**

CONTENTS

Page

MAIN ARTICLES

A Revised List of The Pteridophytes of Nevis
- B.M. Graham, M.H. Rickard 85

Chloroplast DNA and Morphological Variation in the Fern Genus *Platycerium* (Polypodiaceae: Pteridophyta)
- Johannes M. Sandbrink, Roeland C.H.J. Van Ham, Jan Van Brederode 97

Pteridophytes of the State of Veracruz, Medico: New Records
- Mónica Palacios-Rios 119

SHORT NOTES

Chromosome Counts for Two Species of *Gleichenia* subgenus *Mertensia* from Ecuador
- Trevor G. Walker 123

REVIEWS

Spores of The Pteridophyta
- A.C. Jermy 96

Flora Malesiana
- A.C. Jermy 123

The pteridophytes of France and their affinities: systematics, chorology, biology, ecology.
- B. A. Thomas 124

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THE STATUS OF *ASPLENIUM EBERLEI* D.E. MEYER (ASPLENIACEAE: PTERIDOPHYTA)

HELGA RASBACH[1], KURT RASBACH[1], TADEUS REICHSTEIN[2] & RONALD VIANE[3]
[1]Dätscherstr.23, D-7804 Glottertal, Germany;
[2]Institute for Org. Chemistry, St. Johanns-Ring 19, CH-4056 Basel, Switzerland;
[3]Leerstoel voor Morfologie, Systematiek en Ecologie van de Planten, Ledeganckstraat 35, B-9000 Gent, Belgium

Key words: *Asplenium*, Taxonomy, Cytogenetics, Experimental hybridisation.

ABSTRACT

Asplenium eberlei D.E. Meyer is one of the rarest fern taxa: only one small colony of several plants is known from Northern Italy (Dolomites). Detected by the late G. Eberle, it was named after him and first described as a hybrid *Asplenium* × *eberlei* by D.E. Meyer (1962). As it was later shown to produce good spores, the description was emended as *Asplenium eberlei* D.E. Meyer (1967). The author claimed to have counted its chromosomes (2n=144) and concluded that it was an allotetraploid taxon derived from diploid *A.ruta-muraria* L. and *A.seelosii* Leybold. This and other claims have proved to be incorrect.

We have examined the cytology of *A.eberlei* again, taking fixings in the field and of plants raised from spores in the greenhouse, and found it to be diploid. We also made the artificial hybrid of *A. eberlei* with diploid *A. ruta-muraria* which gave full pairing of chromosomes in meiosis, showing that these two morphologically distinct taxa have completely homologous chromosomes, and that *A. eberlei* must be a mutation of diploid *A. ruta-muraria*. Consequently we name it *A. ruta-muraria* L. subsp. *dolomiticum* Lovis & Reichstein var. *eberlei* (D.E. Meyer) Rasbach, Rasbach, Reichstein et Viane **comb. et stat.nov.** holotype: Eberle s.n., 5. Juli 1961, 4 fronds in (B) (=Meyer-2779); and isotype, 3 fronds in (FR).

(Abbreviations for Herbaria follow Holmgren et al., 1990)

INTRODUCTION

Asplenium eberlei is an extremely rare taxon known only from one large block of dolomitic rock in the Dolomites in Northern Italy. It was detected by G. Eberle in 1961, named after him and described first as a hybrid *A.* × *eberlei* D.E. Meyer (1962). Meyer (1962) first assumed it to be a cross of *A. ruta-muraria* L. with *A. seelosii* Leybold, both growing in the vicinity (the latter rare). He later (1967) realized that *A. eberlei* produces good spores and claimed to have counted chromosomes in a root tip, finding it tetraploid with 2n=144 (without giving an illustration). He therefore assumed it to be an *allo*tetraploid species arisen by chromosome doubling in a diploid hybrid between *A. ruta-muraria* L. subsp. *dolomiticum* Lovis & Reichstein (1964) and *A. seelosii* Leybold (see also Eberle 1962, 1967). Meyer even claimed to have found a triploid hybrid "*A. ruta-muraria* × *A. eberlei*, 2n=108". Since the late D.E. Meyer was considered an authority whose first work (1952) was careful and reliable, it took us some time before deciding to check his claims, which all three turned out to be incorrect.

Previously we found other incorrect statements in his publications, e.g. for × *Asplenoceterach badense* D.E. Meyer (1957) [see Rasbach et al. (1989)] , and for *A.* × *nieschalkii* D.E. Meyer (1963) [see Bennert et al. (1988, 1989)].

MATERIAL AND METHODS

Spores used to raise living progeny and for hybridisation

To protect the rare taxon from being destroyed by collectors both G. Eberle and D.E. Meyer fortunately did not disclose the precise locality where they found *A. eberlei.*

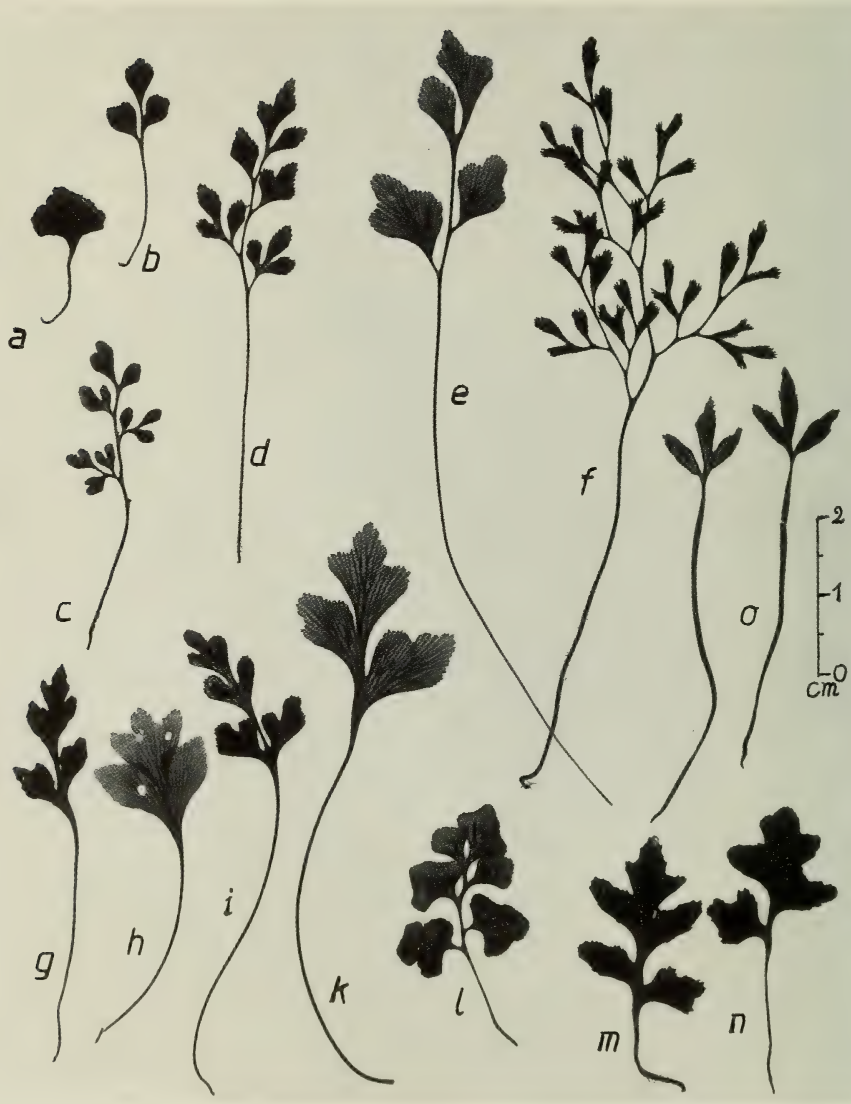


Fig. 1 Silhouettes of fronds (all fertile).

a = *A. ruta-muraria* subsp. *dolomiticum*, TR-5575; Dolomites, 25.9.1981;
b = *A. ruta-muraria* subsp. *dolomiticum*, Ras-505; Dolomites, 14.9.1980;
c = *A. ruta-muraria* subsp. *dolomiticum*, Ras-580; Dolomites, 29.7.1987;
d = *A. ruta--muraria* subsp. *dolomiticum*, Ras-410; Dolomites, 14.9.1986;
e = *A. ruta--muraria* subsp. *dolomiticum*, Ras-528; Dolomites, 14.9.1986;
f = *A. ruta--muraria* subsp. *dolomiticum*, Ras-526; Dolomites, 15.9.1986;
g = *A. eberlei*, D.E. Meyer-3484 (B); Dolomites, Sept. 1965;
h = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Ras 157; Dolomites, 18.9.1980;
i = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Ras-519; Dolomites, 15.9.1986;
k = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Ras-521; Dolomites 18.9.1986;
l = experimental hybrid *A. ruta-muraria* subsp. *dolomiticum* x *A. eberlei*, TR-6646 **2**;
m = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, TR-5302 **2**; progeny from spores;
n = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, TR-5302 **11**; progeny from spores;
o = *A. seelosii*, Ras-496a; Dolomites, 20.7.1986.

Nevertheless a few field botanists (P. Aleksejew, H.W. Bennert and two of us, H. and K. Rasbach) found it independently and showed it to reliable colleagues (H. Melzer, G. Schulze). None of these visitors ever removed a living plant which all remained in their rock fissure. One of us (T.R.) raised living plants (first as TR-2180) from spores collected (Sept. 1965) by D.E. Meyer at the type locality (Meyer-3484) and kindly sent to Basel on 18 Dec. 1967. Sowings were made on 14.1.1968. The progeny was kept in cultivation for c.three years (see Reichstein in Hegi, 1984:236, fig.212) but for the above mentioned reason no cytological examination was performed. Later, new plants (TR-5302) were raised from spores collected at the type locality by H. and K. Rasbach (Ras-158, 15.9.1980). Sowing 8.2.1981 (on Agar-medium) gave ample prothallia, some of which were planted on soil to raise progeny; 15 mature plants were obtained and nearly all were cytologically examined. Meiosis invariably showed $n=36^{II}$ (see Fig.2); in plant no. 4 mitosis in a root tip was also examined and again found diploid with $2n=72$ (Fig. 2). Spores of mature plants were sown again, and the prothallia partly used to raise fresh progeny, partly for hybridisation.

Cultivation

Spores were sown on Agar-medium (Rasbach et al. 1991); the prothallia, when c. 3mm high, were planted in pots with lime free soil (see Rasbach et al. 1983) to which c. 10% pulverized dolomitic rock was added. These pots were kept covered with plastic bowls and watered (dropwise) every day. When sporophytes appeared they were planted in single pots, kept covered until the second or third leaf appeared and then grown open in the cold greenhouse at c. 5-25°C (depending on the season).

Hybridisation

This was done using the method mentioned by Rasbach et al. (1991) and which will be published more extensively in the future. We did two experiments.

TR-6645, on 15.6.1987 using 20 prothallia of *A. eberlei* (TR-6521 = spores Ras-495, sown on 16.10.1986) and 9 prothallia of TR-6522, *A. ruta-muraria* subsp. *dolomiticum* from spores Ras-522 (H. & K. Rasbach, 15.9.1986, coll. at the *locus classicus* of *A. eberlei*, sown 31.1.1987). On 24.8.1987 ten baby sporophytes were planted in pots; most of them succumbed to a fungal infection, only one reached maturity and was *A. eberlei*.

TR-6646, also on 15.6.1987, using 9 prothallia of A. eberlei (TR-5302, sown 31.1.1987) and 16 prothallia of diploid *A. ruta-muraria* subsp. *dolomiticum* (TR-6522, from spores Ras-522, sown 31.1.1987) was more successful. 20 baby sporophytes were planted in pots (24.8.1987) of which 6 reached full size and maturity in June 1988 and were numbered 1 - 6. Judged from their intermediate morphology, plants 2 and 6 were considered hybrids, showing distinct petiolules up to 1.5 mm long and c. 0.3 mm wide (Fig.1). Both hybrids had good, regular spores (Fig.4) and showed $n=36^{II}$ in meiosis (Fig.3), microcharacters are given in Tab. 1. Plants 1, 3, 4 and 5 were *A. eberlei* with deeply pinnatisect leaves, not completely cut to the rachis. No selfs of the second parent (diploid *A. ruta-muraria*) were obtained in the experiment.

Cytological investigation

For cytological investigation premature sporangia were fixed in the field or in the greenhouse, using a fresh mixture of acetic acid and ethanol abs. (1:3). Staining in acetocarmine and squashing was performed as described by Manton (1950:295). Root tips were pretreated in 0.1% aqueous colchicine for 12-14 hours at 4° C. Before squashing, the root tips were softened by partial hydrolysis in 0.1 N hydrochloric acid for 20-30 minutes (depending on thickness) at exactly 60° C. Final analyses of meiosis (spore mother cells) and mitosis (root tips) were made using an Olympus BHS microscope at a magnification of 1000×, with attachment for phase contrast and a drawing tube (Figs. 2 & 3). (All cytological work by H.R.)

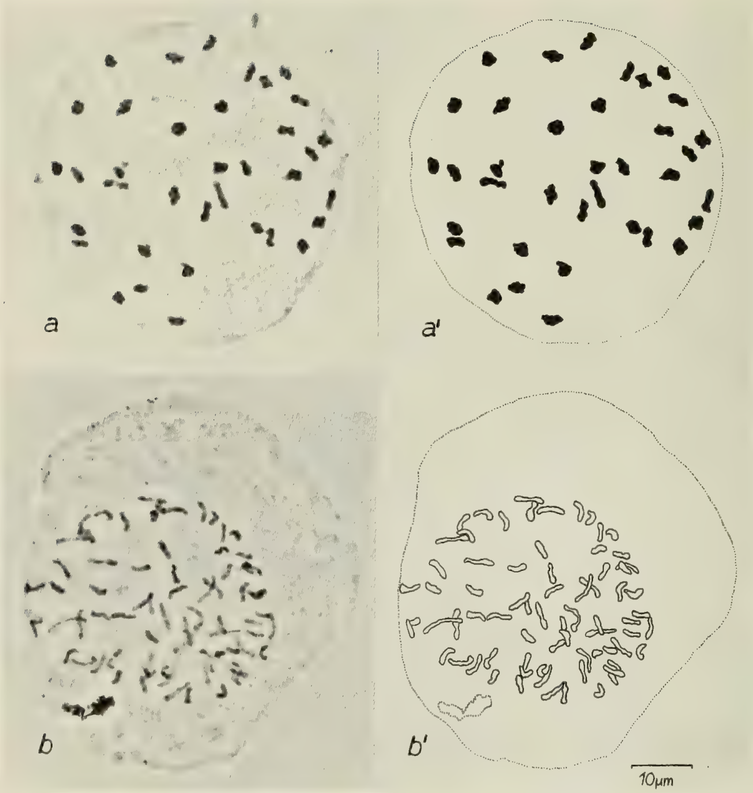


Fig. 2 Cytology

a, b = photographs, a´ , b´ = explanatory diagrams.
a = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, TR-5302, cultivated plant; sporemothercell in meiosis (metaphase I) with n=36^{II}.
b = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, TR-5302 **4**, cultivated plant; mitosis in root tips with 2n=72. Det.: H.R.

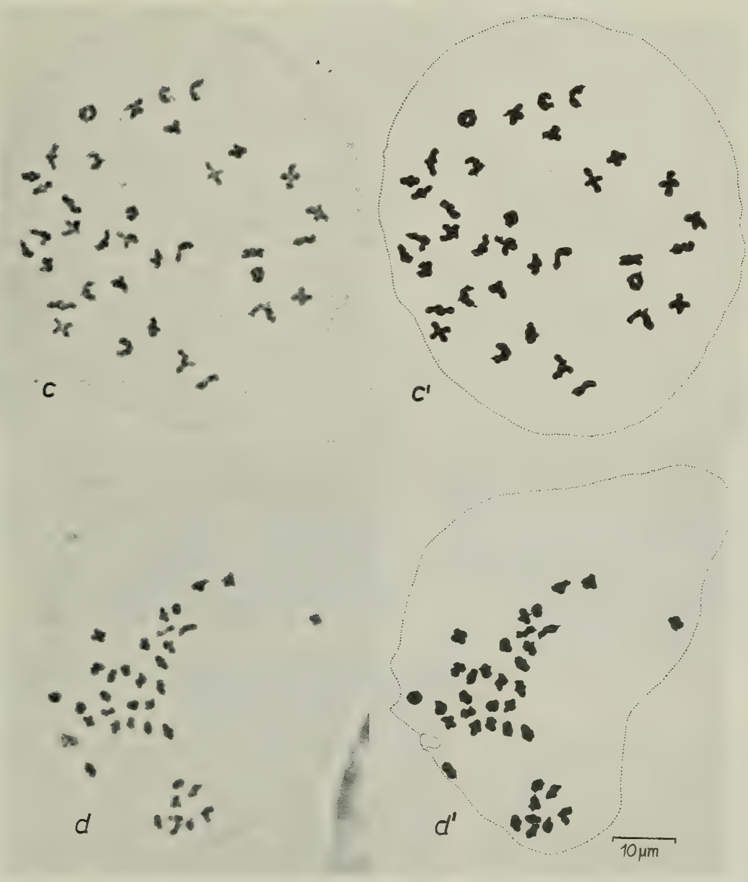


Fig. 3 Cytology

c, d = photographs, c´ , d´ = explanatory diagrams.
c = Experimental hybrid *A. ruta-muraria* subsp. *dolomiticum* x var. *eberlei*, TR-6646 **2**. Sporemothercell in meiosis (diakinesis) with n=36^{II}.
d = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Ras-521 **4**, fixed in the field. Sporemothercell in meiosis (metaphase I) with n=36^{II}. Det.: H.R.

Micromorphology

Methods for micromorphology are those given by R.V. in Demiriz et al. (1990) and by Viane (1990); only untreated, fresh spores were used. Results summarized in Tabs. 1 & 2, and on figs. 4 and 5, are discussed here.

RESULTS

Perispore structure

Mature spores of both diploid and tetraploid *A. ruta-muraria* are lophate, showing several costate ridges set with minute verruculate – echinulate projections. The (largely imperforate) perispore surface is venulate. No significant differences in perispore morphology or structure could be found between any of the subspecific taxa presently recognized (Fig. 4, A-E). Next to the few distinct and alate folds with echinulate crests, mature perispores in *A. seelosii* possess several low and minutely spinulose rims; the areas between the folds (areolas) are perforated by small pori (microfenestrate) and are set with small spinules (echinulose) but a venulose surface pattern is absent (fig. 4, F). Contrary to Meyer's claim (1967:28) Fig. 4 clearly shows that spores of *A. eberlei* are not distinguishable from those of subsp. *dolomiticum*, and that they show no influence of *A. seelosii*. (Juvenile spores of *A. ruta-muraria* and *A. lepidum* may resemble "*seelosii*" spores when observed in the light microscope).

Epidermis patterns

All taxa studied have a similar epidermis pattern (Fig. 5), possessing mainly polocytic stomata [with a few anomocytic ones present besides (Fig. 5 A: top, 5D: top-right)]; however, in *A. seelosii* veins (closer together) are overlain by epidermis cells with distinctly thickened anticlinal cell walls (Fig. 5 F). The epidermis of *A. eberlei* shows no influence of *A. seelosii*.

Though cell sizes can often be used to determine ploidy levels within a species, there appears to be a considerable overlap in stomata size between diploid and tetraploid *A. ruta-muraria*. Exospore size separates the present subspecies more neatly (Tab. 1).

TABLE 1

Exospore and guard cell length (in µm): Mean ± 1 standard deviation, minima and maxima between brackets.

Taxon	Ploidy	Exospore Length	Stomata Length
A. ruta-muraria			
ssp. *dolomiticum* s.l.	2	(29) 38 ± 2.5 (48)	(26) 44 ± 4.0 (61)
var. *dolomiticum*	2	(31) 38 ± 2.4 (48)	(26) 45 ± 4.0 (61)
var. *eberlei*	2	(29) 36 ± 2.7 (43)	(31) 43 ± 4.1 (51)
exp. hybrid	2	(32) 38 ± 2.4 (44)	(33) 44 ± 3.7 (53)
ssp. *ruta-muraria*	4	(34) 44 ± 2.9 (59)	(26) 49 ± 4.9 (64)
A. seelosii	2	(32) 38 ± 2.4 (45)	(30) 44 ± 5.2 (57)

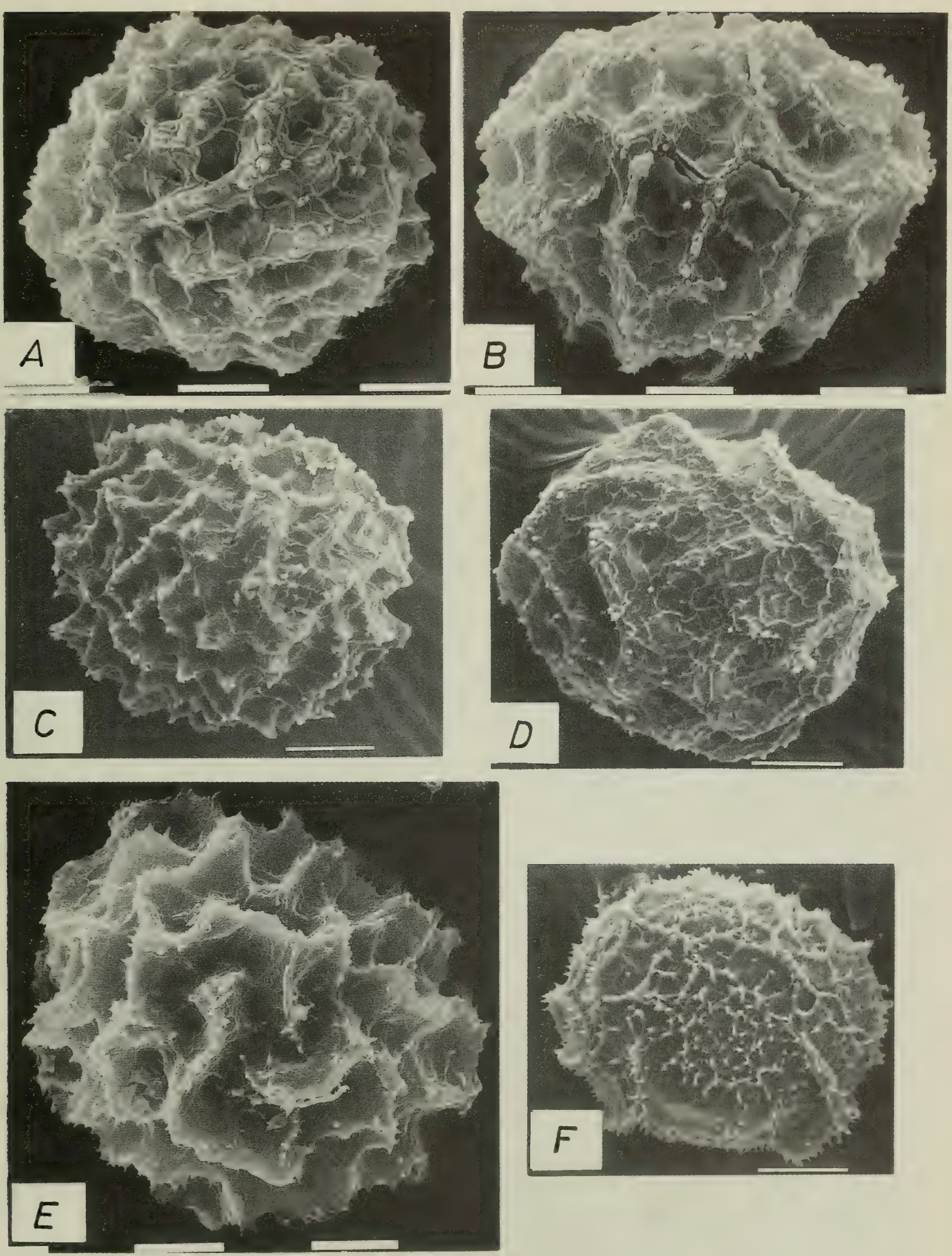


Fig. 4 SEM photographs of spores.

A = *A. ruta-muraria* subsp. *dolomiticum*, Ras-498 (=TR-6518);
B = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Ras-495 (=TR-6521);
C = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Meyer-3484;
D = *A. ruta-muraria* subsp. *dolomiticum* x var. *eberlei*, TR-6646 **(6)**, experimental hybrid;
E = *A. ruta-muraria*, subsp. *ruta-muraria*, TR-4789;
F = *A. seelosii*, Ras-496a.

All spores in c.equatorial view, except A in c. proximal view. Surfaces venulate in A - E. Bar = 10 µm. Photo: R.V.

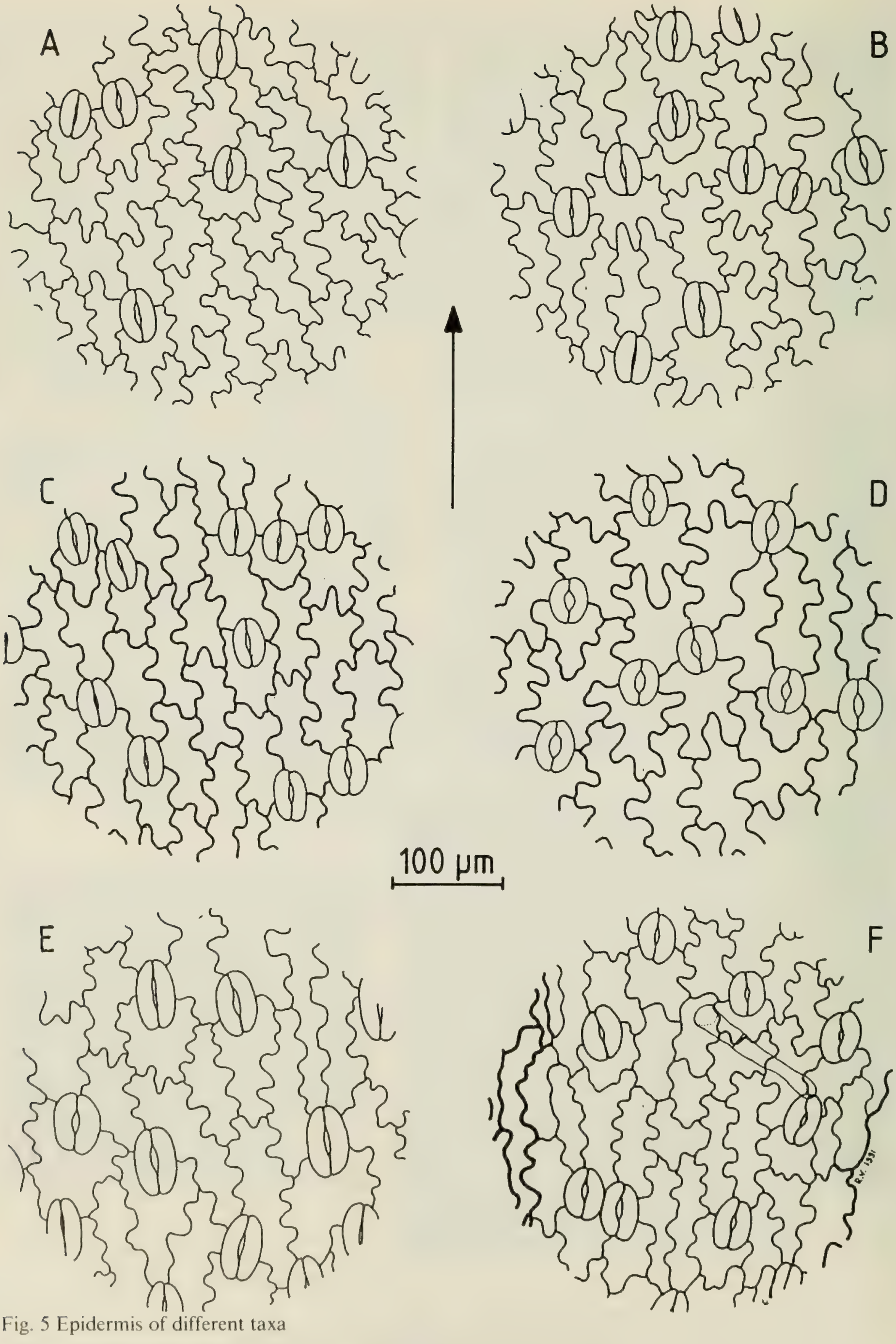


Fig. 5 Epidermis of different taxa

A = *A. ruta-muraria* subsp. *dolomiticum*, RAS-498 (=TR-6518);
B = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, TR-5302, cultivated plant;
C = *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Meyer-3484;
D = exp. hybrid *A. ruta-muraria* subsp. *dolomiticum* × *var. eberlei*, TR-6646 **(6)**;
E = *A. ruta-muraria* subsp. *ruta-muraria*, TR-4789;
F = *A. seelosii*, Ras-496a.

Arrow indicates the direction of a neighbouring vein towards the leaf margin (bar = 100 µm). From this figure one can see that epidermises within *A. ruta-muraria* are essentially similar. Drawing: R.V.

TABLE 2

Cell length (in µm) of individual cells in indusial and epidermal (uniseriate) hairs. Figures are: the mean ± 1 standard deviation, minima and maxima between brackets.

Taxon	Ploidy	Indusial Hair	Epidermal Hair
A. ruta-muraria			
ssp. *dolomiticum* s.l.	2	(37) 108 ± 26 (203)	(16) 42 ± 12 (79)
var. *dolomiticum*	2	(37) 107 ± 27 (203)	(16) 42 ± 12 (79)
var. eberlei	2	(69) 114 ± 25 (202)	(18) 43 ± 13 (77)
exp. hybrid	2	(83) 129 ± 30 (203)	(19) 37 ± 12 (68)
ssp. *ruta-muraria*	4	(45) 111 ± 22 (199)	(24) 51 ± 15 (100)
A. seelosii	2	(41) 63 ± 8 (90)	(34) 70 ± 18 (149)

Indusia

The indusial indument of *A. ruta-muraria* is typical filiform and consists of numerous marginal, uniseriate, multicellular hairs with individual cells narrowly cylindrical and usually longer than 100 µm (Tab. 2). The sub-moniliform leaf indument, quite different from that of the fimbriate indusium, is formed by uniseriate hairs of 4 (-5) cells. The cells composing these hairs are c.30 µm wide (apical cell widest and often up to 45 µm) and have a mean length of c.40-50 µm, making them usually less than twice as long as wide.

Indusia in *A. seelosii* are predominantly glabrous, though each frond studied had at least one indusium with a single or up to a few (marginal and/or dorsal), 2-3 cellular filiform hairs with narrowly cylindrical (usually less than 70 µm long) cells. Another difference from *A. ruta-muraria* is that the indusial indument is similar to that on the leaf: cylindrical (not submoniliform), uniseriate with 3 (-4) cells; composing cells are c.20-30 µm wide (apical not distinctly wider) and usually up to 70 µm long, making them more than twice as long as wide.

The indument of *A. eberlei* cannot be distinguished from that of *A. ruta-muraria* subsp. *dolomiticum* and shows no influence of *A. seelosii.*

OBSERVATIONS AT THE *LOCUS CLASSICUS* OF *ASPLENIUM EBERLEI*

Two of us (H. and K.R.) found the plants in 1980, removed three fronds with spores and photographed the same plant that D.E. Meyer had called "type plant", and which could be identified from photographs in Eberle (1962:112; 1967:344; 1970:114, and personally confirmed by G. Eberle). The surroundings were searched for several hours for other specimens, just as Meyer, Aleksejew and Bennert had already done, but in vain. Later excursions in 1981 and 1982 were again unsuccessful. When the place was revisited in 1986 and 1987, immature sporangia were fixed in the field (Ras-495 = TR-6521, Ras 518, 521) which all turned out to be diploid with $n=36^{II}$ at meiosis (Fig.3). Plant Ras-521 (Fig. 6) is identical with the one which Eberle (1967:345) photographed and also with D.E. Meyer no. 6807, (leg.G.Eberle). Both the late D.E. Meyer and the late G. Eberle kindly confirmed that the place which we found was the *locus classicus* and that our Ras-521 is the same as Meyer no.6807. Furthermore a very good photograph [D.E. Meyer-3729 (B)] of the *locus classicus*, taken by G. Eberle, shows without any doubt this place.

The plant from which the holotype was collected carried c.25 fronds when we first saw it in 1980 but it was much smaller in 1982 and no longer visible in 1986. In 1987 we could still count a total of 8 other plants. No hybrids were found in spite of long searches.

THE TYPE MATERIAL OF *ASPLENIUM EBERLEI* AND OTHER COLLECTIONS

Through the kind help of the curators in B and FR we were able to study all (type) material of this taxon and make the following observations.

In his original description (as a hybrid) Meyer (1962:30, Fig.3) has illustrated the four fronds (Fig.7) of the type collection [G. Eberle s.n. – 5. Juli 1961] deposited in Berlin (B) [he also gave this collection a number of his own: Meyer-2779]. Since the Berlin material was used for the diagnosis it should be considered the holotype according to Article 7.3 of the ICBN (Greuter et al. 1988). The isotype (three fronds), originally in Eberle's personal herbarium, is now deposited in the herbarium of the Forschungsinstitut Senckenberg in Frankfurt (FR) [where it is incorrectly labelled as "holotypus"].

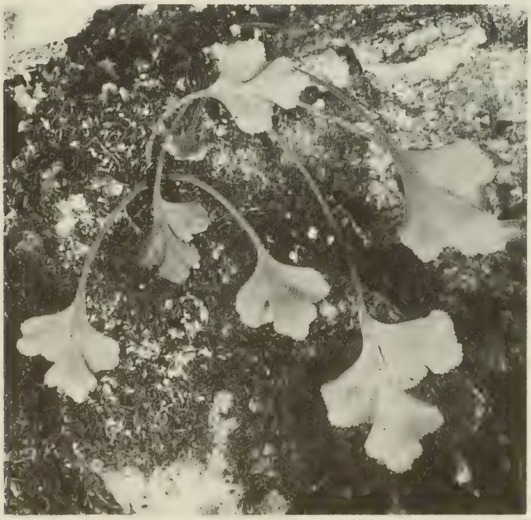
In the diagnosis Meyer wrongly cited the month in which the collection was made as "Juni", however, on the herbarium labels of the type as well as in Meyer's fig. 3 (1962) and in Eberle (1962, 1970) the correct date of 5 July is given.

The sporangia on the fronds of the holotype are not fully ripe, and light microscopical investigation shows that no perispore had yet been formed on the spores (collapsed upon drying but not showing signs of abortion). It is interesting to note that Eberle's own observation about the good condition of the sporangia led him to doubt the hybrid nature of this taxon (1962:113). As a very good observer Eberle (1962:112) also made the following remark: " . . schließlich konnte noch an die Möglichkeit des Vorliegens einer erblichen Sonderform (der Mauerraute) gedacht werden – (" . . one could also consider the possibility that we deal with an aberrant form of wall-rue").

Further investigations persuaded Meyer (1967) to consider this taxon no longer as a hybrid but as an allotetraploid species. Next to the holotype fourteen other collections of *A. eberlei*, all from the same boulder at the *locus classicus*, are deposited in B. All (with exception of 6807, coll.G.Eberle) were collected by Meyer and include: Meyer 3546, 3547, 3548, 3549, 6807 (1962); Meyer 3484, 3530 (1965); Meyer 3550, s.n. (1966); Meyer 3983 (1968); Meyer 5056 (1969); Meyer 5052 (1970); Meyer 6047, 6050 (1972).

Our own herbarium material includes: T. Reichstein 2180, 5302, 5621 (all cultivated from spores);

Rasbach 157, 158 (1980); 495 (1986, 1987); 517-521 (1986); 573 (1987); only single fronds were collected.



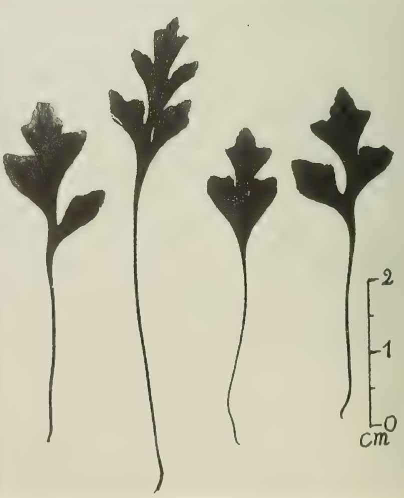


Fig. 6 *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei*, Ras-521, 23.7.1986 at the *locus classicus* (see also Figs. 1 & 3); Photo: K.R.

Fig. 7 Holotype (4 fronds) of *A. ruta-muraria* subsp. *dolomiticum* var. *eberlei* in (B), silhouettes of fronds.

CONCLUSIONS

Our cytological investigations of plants from the locus classicus and of cultivated plants show that *A. eberlei* is a diploid taxon with n=36^{II} in meiosis. Our hybridisation experiment between *A. eberlei* and *A. ruta-muraria* subsp. *dolomiticum* gave ample evidence that the chromosomes of both taxa are homologous: the hybrid clearly shows n=36^{II} in meiosis (Fig. 3). All micromorphological characters (spore size, perispore structure, length of stomata and hairs) in "*A. eberlei*" are indistinguishable from those of diploid *A. ruta-muraria* but some are distinct from those found in *A. seelosii.* Contrary to Meyer's claims no intermediate state between diploid *A. ruta-muraria* and *A. seelosii* could be detected in "*A. eberlei*".

"*A. eberlei*" is obviously just a very distinct mutation in the leaf form/leaf division of diploid *A. ruta-muraria.* Morphologically it is more distinct than any of the varieties described by Laubenburg (1899) and by Christ (1903). "*A. eberlei*" reproduces true from spores (it is not just a modification or ecotype) and forms at least a small natural population. In this respect one might be tempted to treat it as a subspecies of *A. ruta-muraria.*

THE NEW STATUS OF *ASPLENIUM EBERLEI*

Since we were able to prove that "*A. eberlei*" and *A. ruta-muraria* subsp. *dolomiticum* have homologous chromosomes and indistinguishable microcharacters and also that the two taxa are not separated geographically, we consider "*A. eberlei*" a variety of *A. ruta-muraria* subsp. *dolomiticum* and designate it as follows:

***Asplenium ruta-muraria* L. subsp. *dolomiticum* Lovis & Reichstein var.*eberlei* (D.E. Meyer) Rasbach, Rasbach, Reichstein et Viane comb. et stat. nov.** [Basionym: *A. eberlei* Meyer. Ber. Deutsch.Bot.Ges.**72**:29, 1962. Holotype: G. Eberle s.n. (=Meyer-2779) - 5 Juli 1961 (B), isotype (FR)]. It is a diploid sexual taxon not closely related to *A. seelosii.*

DISCUSSION

A. ruta-muraria L. is a very polymorphous species, see Laubenburg (1899:39-40). Christ (1903) reviewed and described with figures 17 varieties of world wide distribution. In Fig. 1 we add some more relatively common extreme forms of diploid *A. ruta-muraria.* Most of these forms are the result of the retention of the juvenile state and of extreme growing conditions which the species is able to tolerate. When transplanted in pots and grown side by side in the greenhouse most of these forms produce similar twice pinnate leaves after 1-2 years of cultivation. A few particularities (shape of pinnules, dentation, density of hairs) sometimes remain and therefore seem to be genetically fixed. All known forms of diploid and tetraploid *A. ruta-muraria,* when fully developed in the greenhouse, will produce at least pinnate fronds with distinct petiolules, and more often twice to three times pinnate leaves. Only var. *eberlei,* even when fully developed, produces pinnatisect leaves (=deeply cut, but not to the rachis; Figs. 1 & 7).

In the hybrid TR-6646, of both varieties of diploid *A. ruta-muraria,* the fully developed leaves are pinnate with the larger pinna shortly stalked, and with petiolules c. 1.5 mm long (Fig. 1).

It is speculative to say anything about the age of the small colony of *A. ruta-muraria var.eberlei* in the Dolomites. Considering the reported facts we think that it most probably arose in situ in historical times as a spontaneous mutation of diploid *A. ruta-muraria.* The first (single) plant may have multiplied partly vegetatively, partly from spores, forming the small colony (8 plants) which exists today. It apparently cannot spread further as a distinct taxon because of introgression with the much more numerous diploid *A. ruta-muraria,* relatively abundant in the surroundings. It is remarkable that *A. ruta-muraria* var. *eberlei* was able to resist extinction, and that it survived and even spread in this limited habitat. This may have been possible by the lack of competition from other plants. It has not spread further since other suitable fissures in the big block are occupied.

ACKNOWLEDGEMENTS

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NEW PTERIDOPHYTE RECORDS FOR MADAGASCAR

FRANCE RAKOTONDRAINIBE
1 Service de Biologie Végétale et de Biochimie, Université d'Antananarivo,
B.P. 906, Antananarivo 101, Madagascar; and Laboratoire de Phytomorphologie,
E.P.H.E., 16 rue Buffon, 75005 Paris, France

ABSTRACT

Bolbitis gemmifera, Trichomanes liberiense, T. erosum var *erosum, T. erosum* var *aerugineum, Asplenium gemmiferum* and *Amphineuron opulentum* are recorded for the first time in Madagascar.

INTRODUCTION

Six new pteridophyte records for Madagascar are reported. Four of these are the result of recent collecting trips to the Manongarivo massif, an area of difficult access in the northwestern part of Madagascar that previously had been very little explored. The remaining two records are from more frequently botanized areas. None of the six species were cited either by Christensen (1932), Tardieu-Blot (1951-1971) or by any other authors.

Bolbitis gemmifera (Hieron.) Christ. Madagascar: Antsiranana Prov., Manongarivo massif, shaded forest floor, on the banks of the Antsahamanara River, 14° 06′ S, 48° 17′ E, 250m, *F. Rakotondrainibe 1046* (P); Bekolosy Mtn., 14° 05′ S, 48° 17′ E, several large colonies between 450-750m, terrestrial, in moist areas on rocks, *F. Rakotondrainibe 1044, 1230* (P), *1045, 1228, 1229* (Univ. d'Antananarivo). This species is characterized by having all the pinnae free and the terminal pinnae bearing a gemma at the base. Known from tropical Africa (Tardieu-Blot, 1964), but previously unreported from Madagascar.

Trichomanes liberiense Copeland. Madagascar: Antsiranana Prov., Manongarivo massif, lithophyte and low-level epiphyte in forest, Antsahamanara River, 14° 06′ S, 48° 17′ E, 250m, *F. Rakotondrainibe 1094* (Univ. d'Antananarivo); Bekolosy Mtn., 14° 05′ S, 48° 17′ E, 500m, *F. Rakotondrainibe 1345* (Univ. d'Antananarivo), *1346* (P). This species is easily recognized by its entire, elliptic or obovate lamina, and by the presence of a black silky indumentum along the margins. It is closely related to *T. montanum* Hook., from which it differs by the form of its conical indusia, which have entire, rounded valves, and by the absence of false veins. Previously known from Cameroon, Liberia, Ivory Coast, and Nigeria (Tardieu-Blot, 1964).

Trichomanes erosum Willd. var. ***erosum***. Madagascar: Antsiranana Prov., Manongarivo massif, Bekolosy Mtn., lithophyte and low-level epiphyte in forest, 14° 05′ S, 48° 17′ E, 950m, *F. Rakotondrainibe 1095, 1096* (Univ. d'Antananarivo); Antsatrotro Mtn., 14° 08′ S, 48° 24′ E, 1000m, *F. Rakotondrainibe 1349* (Univ. d'Antananarivo). This species is characterized by its lanceolate, entire to irregularly crenate lamina, the absence of a black silky indumentum along the margin, and by the presence of false lateral veins and a submarginal vein. Previously known from Zimbabwe, Mozambique, Tanzania, Zaire, Angola, Cameroon, Nigeria, Ghana, Liberia, Sierra Leone, Comoros and Seychelles (Schelpe, 1970).

Trichomanes erosum Willd. var. ***aerugineum*** (Bosch) Bonap. Madagascar: Antsiranana Prov., Manongarivo massif, Bekolosy Mtn., lithophyte and low-level epiphyte in moist, shaded forest, 14° 05′ S, 48° 17′ E, *F. Rakotondrainibe 1097* (Univ. d'Antananarivo); Antsatrotro Mtn., 14° 08′ S, 48° 24′ E, 1600m, *F. Rakotondrainibe 1353* (P). This taxon differs from the typical variety by the lanceolate, but clearly pinnatifid, lamina. Previously known from Mozambique, South Africa, Tanzania, Zaire, Cameroon, Ivory Coast, Liberia, Sierra Leone, and Fernando Po (Schelpe, 1970).

Asplenium gemmiferum Schrader. Madagascar: Fianarantsoa Prov., Ranomafana Natl. Park, along river banks, lithophytic on humus covered rocks in forest, 600-700m, 21° 15′ S, 47° 27′ E, *G. Rahajasoa et al. 11,60; F. Rakotondrainibe 233* (Univ. d'Antananarivo). This species is closely related to *A. anisophyllum* Kunze, from which it differs by having thin, elongated sori occurring throughout almost all of the lamina between the margin and the costa; in *A. anisophyllum* the sori are very thick and short. Previously known from Zimbabwe, Malawi, Mozambique, South Africa, E. Tropical Africa, and E. Zaire (Schelpe, 1970).

Amphineuron opulentum (Kaulf.) Holttum [=*Thelypteris opulenta* (Kaulf.) Fosberg]. Madagascar: Toamasina Prov., Ile Sainte-Marie, near the airport, in a disturbed area, in slightly shaded, sandy ground, 17° 05′ S, 49° 48′ E, 5m, *F. Rakotondrainibe 740, 741* (P), *742* (Univ. d'Antananarivo). This species is easily recognized by its deeply 2-pinnatifid lamina with the basal pinnae not reduced, 1 pair of veins anastomosing below the sinus between the pinnae lobes, and dorsal yellow glands present on the veins. Previously known from Mozambique, East tropical Africa, and from Sri Lanka to the Philippines (Schelpe, 1970). Currently becoming one of the most widespread weedy ferns in South America (R.C. Moran, per. com.) This species might be a recent immigrant to Madagascar.

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REGINALD KAYE

With the deepest regret, we have to inform you that on Thirty-first August, 1992 our great friend and colleague died peacefully at home, sitting listening to a Promenade concert.

We give our tenderest condolences to his family at Waithman's Nurseries.

Further tributes are planned for the *Bulletin* and *Pteridologist*.

CYTOTAXONOMIC NOTES ON MEMBERS OF VENEZUELAN GLEICHENIACEAE

TREVOR G. WALKER
Department of Biological and Nutritional Sciences,
The University of Newcastle upon Tyne
Newcastle upon Tyne NE1 7RU, U.K.

&

FRANCISCO ORTEGA
Herbario Universitario, UNELLEZ – Guanare, Edo.
Portuguesa 3323, Venezuela

ABSTRACT

Chromosome counts are recorded for six species of Gleicheniaceae from Venezuela. Four of these are first reports. Counts for the other two species (*Dicranopteris pectinata* & *Gleichenia bifida*) help to confirm the cytological constancy of these species over a wide geographical range. The suggested closeness of *G. cundinamarcensis, G. costaricensis* and *G. revoluta* is confirmed on both morphological and cytological grounds whereas the putative conspecific status of *G. brittonii* and *G. rubiginosa* is not tenable.

INTRODUCTION

In 1990 the first author (TGW) spent September in Venezuela based at the Universidad Nacional Experimental de los Llanos Ezequiel Zamora (= UNELLEZ) at Guanare in the State of Portuguesa gathering material for cytotaxonomic studies of some Venezuelan ferns in collaboration with Francisco Ortega the co-author. Meiotic fixations were made in the field of members of the Gleicheniaceae; a group of ferns that is notoriously difficult to transplant or grow successfully from spores. Examination of these fixations is now complete. The results have prompted an investigation into the comparative morphology of two of the species in relation to allegedly closely related non-Venezuelan taxa.

MATERIALS AND METHODS

Sporangia were fixed in three parts absolute ethanol to one part glacial acetic acid. They were refrigerated until a few days before returning (TGW) to Newcastle-upon-Tyne when they were transferred to 75% ethanol in which they were stored. The cells were examined by the standard squash method using aceto-carmine as stain. Identifications were made by FO.

RESULTS

Venezuela is divided politically into a number of States (Fig. 1) and has an excellent network of roads many of whose banks provide suitable habitats for members of the Gleicheniaceae. The time factor restricted our collecting to parts of the Andes. Here differences in altitude and aspect give rise to great environmental variety, especially in regard to rainfall and temperature. Some species are confined to a relatively narrow altitudinal belt within a comparatively restricted area in the country. Others show much greater altitudinal tolerances and are found over a much wider geographical range as may be seen from the distributional data quoted for each of the species examined here.

Gleichenia in the widest sense forms a very distinctive and ancient group of ferns of which there are about 130 species distributed throughout the tropics. Despite their highly characteristic appearance, which sets them off from other ferns, it is clear that they do not form a homogeneous entity and fundamental revisions of the group were made by Copeland (1947) and Holttum (1957). The former recognised four genera, namely *Gleichenia*, *Hicriopteris, Sticherus* and *Dicranopteris* whilst Holttum concluded that there were two genera, *Gleichenia* and *Dicranopteris*, which were further split into three and two subgenera respectively. The existence of these two revisions has been reflected in the nomenclature adopted by various workers on the American taxa e.g. Tryon and Tryon (1982), Walker (1985) and Jermy and Walker (1985) follow Holttum, whilst Smith (1985) and Ortega (1991) follow Copeland. The cytological facts are most in accord with Holttum's system, since each subgenus has its own characteristic basic chromosome number which is different from that of all the others (Walker 1966, 1973). The five species whose cytology is reported here (Table 1) belong to only two subgenera, namely *Dicranopteris* subgenus *Acropterygium* (= *Dicranopteris p.p. sensu* Copeland) and *Gleichenia* subgenus *Mertensia* (= *Sticherus*).

NOTES ON INDIVIDUAL SPECIES

The information on the ranges of the species in Venezuela have been taken from Smith (1985). The numbers in parentheses after the names of the States refer to the map in Fig. 1.

1. *Dicranopteris pectinata*

This is the only member of subgenus *Acropterygium* and has the very distinctive chrommosome number of n = 43, as had also specimens from Jamaica (Walker 1966), Trinidad (Walker 1985) and Mexico (Smith and Mickel 1977). Sorsa (1968) reported n = 44 for Puerto Rican specimens, but elsewhere they have proved to be n = 43.

It is one of the widest ranging of the New World members of the family, extending throughout the American tropics and subtropics. Within Venezuela it shows a wide altitudinal tolerance, from 150m to 1800m and is recorded from half the States, namely Amazonas (21), Aragua (12), Bolivar (20), Falcon (2), Lara (3), Miranda (13), Portuguesa (5), Sucre (17), Trujillo (4), Yaracuy (10) and Zulia (1).

2. *Gleicheina bifida*

The most abundant and, with the widest distribution of the American species of *Gleichenia*, it extends through the Caribbean, Central America and most of tropical South America. In Venezuela *G. bifida* ranges from 550m to 2500m and has been recorded from about two thirds of the States, namely Amazonas (21), Aragua (12), Barinas (7), Bolivar (20), Carabobo (11), Falcon (2), Lara (3), Yaracuy (10), Merida (6), Miranda (13), Monagas (18), Portuguesa (5), Sucre (17) and Tachira (8). Previous records for this species in the strict sense have shown it to be diploid with n = 34 in Jamaica (Walker 1966, 1973), Trinidad (Walker 1985), Mexico (Smith and Mickel 1977), Puerto Rico (Sorsa 1968), Costa Rica (Walker 1990) and Ecuador (Walker 1992). Venezuelan specimens are likewise diploid with n = 34. A tetraploid species, *G. interjecta* Jermy & T. Walker, together with two triploid hybrids, namely, *G. x pseudobifida* Jermy & T. Walker and *G. x subremota* Jermy & T. Walker all of which involve *G. bifida s.s.* in their parentage were described from Trinidad (Jermy & Walker 1985). Although these were looked for in Venezuela none was found.

3. *G. cundinamarcensis*

This is both altitudinally and geographically the most restricted of the species reported here. It occurs between 2000m and 2500m where it not only colonizes roadside banks but also extends into the cloud forest. Smith (1985) records it only from Merida (6) but our specimens came from adjoining Trujillo (4) thus slightly extending its range.

The status of *G. cundinamarcensis* is interlinked with that of *G. costaricensis* from Costa Rica and Panama and of both of these with *G. revoluta* H.B.K., originally described from Ecuador. Thus Smith (1985) and Tryon and Stolze (1989) expressed the view that *G. revoluta* is probably synonymous with *G. costaricensis.* Lellinger (1989) does not list *G. revoluta* separately in his monograph of the ferns and fern allies of Costa Rica, Panama and the

Choco. However, under the entry for *G. costaricensis* Lellinger states that this species is very closely related to *G. revoluta* which has stiffer marginal setae in the lamina scales and in addition the rhizome scales are borne on low protuberances.

Smith (1985) also suggests that *G. costaricensis* is closely allied to *G. cundinamarcensis* of Venezuela. We have examined our gatherings of these two species and find that they can hardly be separated in details of the scales of both the buds and of the abaxial surfaces of the lamina axes. On the other hand, the plentiful scales on the adaxial surfaces in *G. costaricensis* are highly distinctive in being narrowly elongated and ending in long setae up to twice the length of the scale proper. Whilst such scales were absent from some specimens of *G. cundinamarcensis* they were present, albeit very sparsely, in other individuals. The cytology of these three species has been examined by TGW at different times viz. *G. costaricensis* (Walker 1990), *G. revoluta* (Walker 1992) and *G. cundinamarcensis* (pres. comm.). All proved to be tetraploid with n = 68. The case for the three species being, at the very least, closely related is greatly strengthened by a more detailed examination of the cytological preparations which show that all the bivalents are not of a uniform size (Fig. 2) unlike the situation in all the diploid species that have been studied. Whilst it is true that different sized bivalents had also been noted in *G. interjecta* (Walker 1985), in that case there were approximately 34 large and 34 smaller bivalents suggesting that this tetraploid had been derived by hybridization and chromosome doubling from a small-chromosomed and a large-chromosomed species. What is distinctive in the three tetraploids reported here is that there are only a relatively few (c.9 - 11) small bivalents in each cell and this is the same for each of the three taxa (Fig. 2a & b). Here, therefore, we have a most unusual cytological feature which is found in all three tetraploids, arguing strongly that they are intimately related to one another. If *G. revoluta, G. costaricensis* and *G. cundinamarcensis* are not to be regarded as synonymous then they are in all probability geographical variants of the one species – a situation which, according to one's view, may or may not justify separate names.

4. *G. nuda*

This species is unique among the fourteen taxa of *Gleichenia* in Venezuela in lacking scales on any of the aerial parts except of the buds. It has a very restricted geographical range, being apparently confined to Venezuela, although Maxon (1922) tentatively ascribed a Colombian specimen to it. Within Venezuela the distribution is also limited, occurring in the States of Aragua (12), Merida (6) and Miranda (13) between 600 and 2250m in the open in montane rain forest (Smith 1985). Our specimens extended the altitudinal range a little, being collected at 2350m. Here they were growing in small thickets in open areas in forest in the Sierra Nevada National Park. This forest has developed since the original tree cover was cut down about a century ago and now has virtually all the characteristics of authentic cloud forest.

Cytological preparations were obtained from one plant. Although of poor quality and not allowing an accurate determination, they were adequate to establish this taxon as a diploid with approximately 34 bivalents at meiosis.

5. *G. pallescens*

The conspicuous large white persistent scales which are borne on the primary and secondary rachises, but lacking in the foliose portion, make this an easily recognisable species. Smith (1985) recorded it as being a plant of mid elevations, ranging from 1150m to 1560m in Venezuela in the States of Amazonas (21), Aragua (12), Bolivar (20), Falcon (2), Lara/ Yaracuy (3/10), Merida (6), Portuguesa (5), Trujillo (4) and Zulia (1). Our specimens not only extend the list of States to include Barinas (7) but also greatly increase the altitudinal range up to 2500m.

Our specimens from both Barinas and Trujillo were diploid with n = 34.

6. ***G. rubiginosa***

This is a plant of high elevations, ranging from 1700m to 2900m and is recorded with confidence from only five States, these being Aragua (12), Merida (6), Monagas (18), Sucre (17) and Trujillo (4). However, this does not represent a more or less continuous distribution but a somewhat disjunct one of three areas.

Smith (1985) considers that *G. brittonii* (Maxon) C. Chr. (or *Dicranopteris brittonii* Maxon as Smith refers to it) is nearly identical to *G. rubiginosa.* Although we have not seen the type specimens, TGW has made gatherings of *G. brittonii* from the locus classicus of El Tucuche in Trinidad. A comparison of these with our gatherings of *G. rubiginosa* show significant differences in respect of the scales on different parts of the plant and the density of the segments on the axis (Table 2). Indeed, about the only features in common are the high profile shown by the veins on the underside of the segments and the fact that *G. brittonii* is diploid with n = 34 (Walker 1985) as is also *G. rubiginosa.*

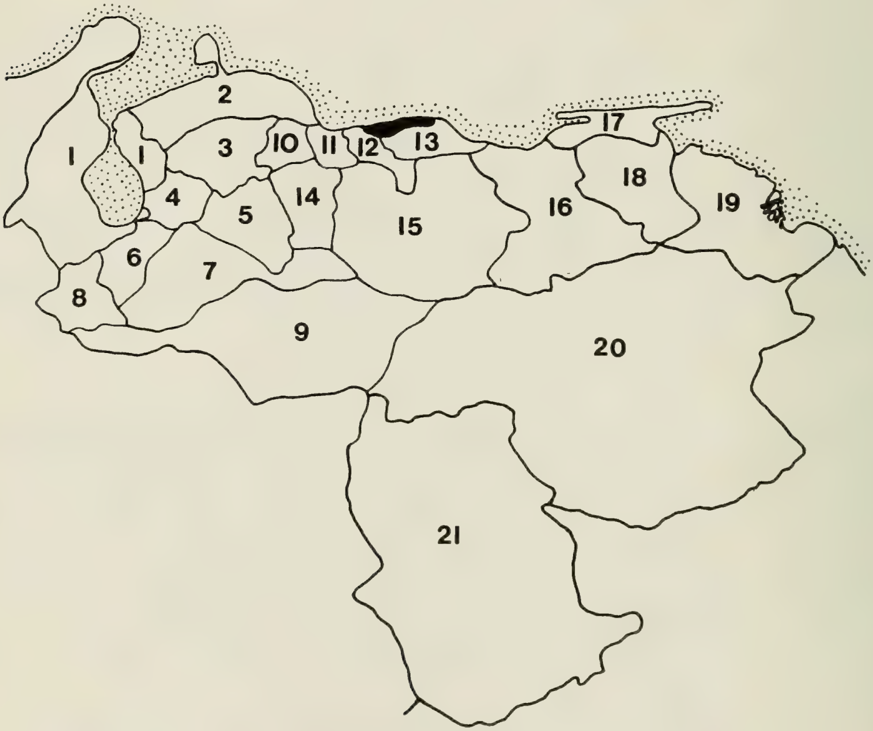

FIGURE 1. Map showing the States of Venezuela.
1 Zulia. 2 Falcon. 3 Lara. 4 Trujillo. 5 Portuguesa. 6 Merida. 7 Barinas. 8 Tachira. 9 Apure.
10 Yaracuy. 11 Carabobo. 12 Aragua. 13 Miranda. 14 Cojedes. 15 Guarico. 16 Anzoategui. 17 Sucre.
18 Monagas. 19 Delta Amacuro. 20 Bolivar. 21 Amazonas. Solid Black: Federal Region.

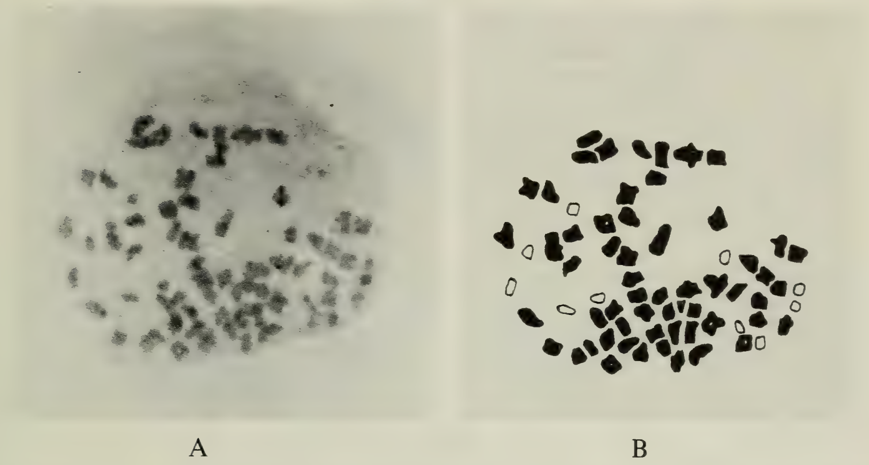

FIGURE 2.A. Metaphase 1 in *Gleichenia cundinamarcensis* showing n = 68, x 1000. B. Explanatory diagram with the markedly smaller bivalents in outline and the standard bivalents solid black.

TABLE 1

Cytologically investigated taxa of Gleicheniaceae from Venezuela. Full details of each locality are cited once only.

Taxon	Coll. No.	Locality	Chromosome Number (n)	Ploidy
1. *Dicranopteris pectinata* (Willd.) Underw.	15105	Felspar mine, El Celoso, Edo. Barinas, c. 1500m	43	2
2. *Gleichenia bifida* (Willd.) Spreng.	15106	El Celoso	34	2
	15114	El Celoso	34	2
3. *G. cundinamarcensis* Hieron.	15259	Paramo of Guaramacal, Edo. Trujillo, c.2500m	68	4
	15260	Guaramacal	68	4
4. *G. nuda* (Reichardt) Moore	15183	Sierra Nevada Nat. Park, Edo. Merida, 2350m	c.34	2
5. *G. pallescens* Mett.	15111	El Celoso	34	2
	15254	Guaramacal	34	2
	15255	Guaramacal	34	2
	15258	Guaramacal	34	2
6. *G. rubiginosa* Mett.	15349	Guaramacal	34	2
	15251	Guaramacal	34	2
	15252	Guaramacal	34	2

TABLE 2

Comparative features of *Gleichenia brittonii* and *G. rubiginosa*

	G. brittonii	***G. rubiginosa***
1. Bud scales	Chestnut brown, with short straight marginal hairs	Chestnut brown, with marginal hairs (often) greatly reflexed up to 3x length of those of *G. brittonii.*
2. Rachis scales	Light brown, with short marginal hairs. Terminating in 1 or 2 hairs less than 1/5 length of scale	Light brown, with marginal hairs 2 - 3x length of those of *G. brittonni.* Terminating in small tuft of hairs up to ½ length of the scale.
3. Costa scales		
a) abaxial	Virtually a branched multicellular hair	Similar in morphology to the rachis scales but c. ½ the size
b) adaxial	Absent	Reduced to a few cells bearing long marginal hairs.
4. Vein scales	Reduced to branched hairs	Similar to, but more abundant than in, *G. brittonii.*
5. Segment density*	12-14 pairs of segments per 5cm length of rachis	8-10 pairs of segments per 5cm length of rachis.
6. Veins on abaxial surface	high profile	high profile
7. Cytology	n = 34, diploid	n = 34, diploid

* Because of differing shapes and spacing of segments, the commonly quoted measurements of the width and the distance apart of the segments do not always provide an accurate picture. Here the number of pairs of segments have been counted for 5cm lengths of the rachis, taken at the mid-point of the lamina, to give the segment density.

CONCLUSIONS

Gleichenia subgenus *Mertensia* encompasses more than 90 species worldwide of which about 40 occur in the American tropics (Tryon & Tryon 1982). Chromosome counts for four of the species considered here, namely for *G. cundinamarcensis* (4x), *G. nuda* (2x), *G. pallescens* (2x), and *G. rubiginosa* (2x) are first reports. This brings the total of New World members of this subgenus which have been cytologically examined to about a third of the total, comprising 12 diploid and 5 tetraploid species (for listing see Walker 1990, and Walker 1992). In the case of the other two species, namely *D. pectinata* and *G. bifida*, these additional records help to confirm the cytological constancy of these plants over a wide geographical range.

Morphological studies confirm the closeness of *G. cundinamarcensis, G. costaricensis* and *G. revoluta* as had been previously suggested in the literature and this closeness has been reinforced by the sharing of a cytological pecularity in the form of a restricted number of small bivalents. In contrast, the alleged conspecific status of *G. brittonii* and *G. rubiginosa* has been shown to be untenable.

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SOME NEW OBSERVATIONS ON THE FERN FLORA OF THE AZORES

H. WILFRIED BENNERT, ANTJE GIERS, SONJA GÜLDENPENNING,
ALEXANDRA HERBIK & ANJA KATHEDER
Spezielle Botanik, Ruhyr-Universität Bochum, Universitätsstrasse 150,
D-4630 Bochum 1, Germany

ABSTRACT

New observations on the fern flora of the Azores are given. *Asplenium* x *sarniense* (= *A. adiantum-nigrum* x *A. obovatum* subsp. *lanceolatum*) is recorded for the Azores, and the whole Macaronesian Islands, for the first time. *Dryopteris crispifolia* is recorded for São Miguel for the first time. A new locality for the very rare *Grammitis jungermannioides* is recorded for Pico.

INTRODUCTION

In spring 1991 we spent two weeks on the Islands of São Miguel and Pico studying the fern flora of the Azores. We recorded 57 different pteridophyte species and hybrids out of a total of 83 taxa that are listed in literature (Carvalho e Vasconcellos 1968; Ward 1968, 1970; Jalas & Suominen 1972; Wilmanns & Rasbach 1973; Rasbach et al. 1974; Gibby et al. 1977; Lovis et al. 1977; Fraser-Jenkins 1981; Fernandes 1984; Gibby 1985; Hansen & Sunding 1985; Derrick et al. 1987). In the following we report on some remarkable observations that were made.

MATERIALS AND METHODS

A small portable microscope with a calibrated eyepiece was used for examining and measuring spores in the field. In this way, hybrids could be detected by their aborted spores, and different cytotypes of aggregate species (like *Asplenium trichomanes* L.) or diploid and tetraploid taxa of closely related and morphologically similar species complexes (like *Asplenium adiantum-nigrum* L. and *A. onopteris* L.) could be separated (see Bennert et al. 1990).

RESULTS

Asplenium* x *sarniense Sleep, the hybrid between *A. adiantum-nigrum* and *A. obovatum* Viv. subsp. *lanceolatum* (Fiori) Pinto da Silva (= *A. billotii* F.W. Schultz), was first discovered in 1971 in Guernsey growing in sandy loam in a tall hedgebank by a roadside (Sleep 1971). It forms rather easily at places where the parent species grow together in larger intermixed populations, preferably in the west of this Island (Sleep & Ryan 1972, Palmer 1989, Bennert et al. 1991). On the mainland it is known from scattered localities in the north-western part of France (Massif armoricain) which are under the influence of an Atlantic climate regime (Bennert et al. 1991). The cytology of a plant from the French Département de la Manche was published recently (Bennert et al. 1991). The meiosis showed 37^{II} and 70^{I} which is in complete agreement with the assumed origin of its parents (*A. adiantum-nigrum* is an allotetraploid, *A. obovatum* subsp. *lanceolatum* an autotetraploid taxon).

Asplenium x *sarniense* was found on the south coast of Pico, above Almagreira (near Lajes do Pico), at an elevation of 220 m. The single hybrid plant grew together with its parents and *A. trichomanes* subsp. *quadrivalens* on a lava wall by the roadside. It was collected (8.5.1991) and is now in cultivation in the greenhouse of the University of Bochum (as WB SP 52/91). Its cytology has yet not been checked as new leaves have failed to develop. Its identity, however, is not in doubt as the plant is morphologically intermediate between *A. adiantum-nigrum* and *A. obovatum* subsp. *lanceolatum* and produces completely aborted spores.

This hybrid was hitherto unknown from the Macaronesian Islands but its occurrence on the Azores is not surprising. Its parents are associated occasionally as we have seen on both Islands: São Miguel and Pico. On the other larger archipelagos of the Macaronesian Islands, *A. adiantum-nigrum* is a rare plant. It was only very recently found on Madeira (Rasbach et al. 1990).

Dryopteris crispifolia Rasbach, Reichstein & Vida is an allotetraploid species, being derived from the diploids *D. aemula* and *D. azorica* (Gibby et al. 1977). It is endemic to the Azores and was previously known only from Faial and Pico (Gibby et al. 1977, Fraser-Jenkins 1981, Hansen & Sunding 1985). We discovered it at a single locality on São Miguel. On this Island not many sites suitable for the growth of *Dryopteris crispifolia* have been left undestroyed, because most parts of the Island are either used as pasture grounds or afforested with alien timber species, mainly *Cryptomeria japonica. Dryopteris crispifolia* was found at the lower slopes of the Lagoa do Congro, a small crater lake situated west of Furnas and northeast of Vila Franca do Campo. The upper slopes bear mainly cultivated trees and shrubs like *Cryptomeria japonica, Hydrangea macrophylla, Rhododendron indicum* and even Central European species like *Quercus robur* and *Acer campestre.* The lower part of the crater offers a much more natural impression. Dominant trees are *Pittosporum undulatum* and an old stand of *Ocotea foetens,* which seems to be the first record of this species for the Azores. The crater lake itself (400 m altitude) is rather difficult to access. About 5 m above the lake we discovered one large and several small plants of *Dryopteris crispifolia* (51/91, herbarium W.B., 3.5.1991). In the vicinity we recorded *D. aemula, D. azorica, Hymenophyllum tunbrigense* (epiphytic on trunks) and a small colony of *Trichomanes speciosum.* No *Dryopteris* hybrids were discovered.

Grammitis jungermannioides (Klotzsch) Ching was reported by Rasbach et al. (1974) as new to the flora of the Azores. They found a single plant of this species and presented a map where the locality in the western part of the Island of Pico is shown. In May 1991 we succeeded in discovering a new locality east of Mount Pico. Right next to the road about 1 km west of the Lagoa do Caiado (c. 800 m alt.) there was a small area of almost natural *Juniperion brevifoliae* woodland (see Sjögren 1973). At the edge of this wood, which was separated from the neighbouring grazing land by a stone wall, *Grammitis jungermannioides* grew on a c. 10 cm thick branch of a treelike *Erica scoparia* subsp. *azorica* at a height of about 1.5 m (69/91, herbarium W.B., 6.5.1991). In spite of an intensive search only a single plant was detected. Other fern epiphytes associated with *G. jungermannioides* were *Hymenophyllum tunbrigense* and *Elaphoglossum semicylindricum. Erica scoparia* subsp. *azorica, Juniperus brevifolia* subsp. *azorica* and *Vaccinium cylindraceum* were the dominating woody plants. All trees and shrubs were densely covered with epiphytes and thick carpets of mosses and huge rhizomes of *Culcita macrocarpa* stretched all over the ground. Other fern species, partly exhibiting luxurious growth, included *Dryopteris aemula, D. azorica* and *D. crispifolia.*

In a very recent paper Hansen (1992) reports 4 new localities of *G. jungermannioides* near the Lagoa do Caiado (Pico). He also succeeded in finding another *Grammitis* species previously unknown from the Azores which was determined as *G. ebenina.* According to Bishop (1988), who suggested the separation of the new genus *Ceradenia* from *Grammitis, G. jungermannioides* bears the name *Ceradenia jungermannioides* (Klotzsch) Bishop.

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NOTES FOR CONTRIBUTORS

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VOLUME 14 PART 4 **1992**

CONTENTS

Page

MAIN ARTICLES

The status of *Asplenium eberlei* D.E. Meyer (Aspleniaceae: Pteridophyta)
- Helga Rasbach, Kurt Rasbach, Tadeus Reichstein & Ronald Viane 125

New pteridophyte records for Madagascar
- France Rakotondrainibe 137

Cytotaxonomic notes on members of Venezuelan Gleicheniaceae
- Trevor G. Walker & Francisco Ortega 139

Some new observations on the fern flora of the Azores
- H. Wilfried Bennert, Antje Giers, Sonja Güldenpenning,
Alexandra Herbik & Anja Katheder 146

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